

SPECIES INTERACTIONS ASSOCIATED WITH
RED-COCKADED WOODPECKER CAVITIES AT
TWO FORESTS IN NORTHERN PENINSULAR FLORIDA

By

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I combined observational, experimental, and mathematical-modeling approaches to examine the effects of heterospecific cavity occupation on the red-cockaded woodpecker (*Picoides borealis*), an endangered cooperative breeder, at Camp Blanding Training Site (CBTS) and Goethe State Forest (GSF). *Picoides borealis* group size, an index of group-fitness, correlated positively with cavity number/territory and negatively with heterospecific occupancy (number of cavities/territory occupied by kleptoparasites), indicating that group size was cavity limited and that kleptoparasites exacerbated this limitation. However, the relative abundance of the two primary kleptoparasites, red-bellied woodpeckers (*Melanerpes carolinus*) and southern flying squirrels (*Glaucomys volans*), and their correlations with group size, differed between study forests. *Melanerpes carolinus* occupancy was similar at each forest (~0.75 cavities/cluster), but

G. volans occupancy was three times greater at CBTS (0.87 vs. 0.28). Correspondingly, at CBTS, group size was negatively correlated with *G. volans* occupancy and uncorrelated with *M. carolinus* occupancy. At GSF, group size was negatively correlated with *M. carolinus* occupancy and uncorrelated with *G. volans* occupancy. These findings, and field observations of interspecific interactions, suggested a transitive dominance hierarchy: *G. volans* > *M. carolinus* > *P. borealis*. A before-after control-removal experiment at CBTS supported this hypothesis; *M. carolinus* occupancy increased significantly in response to *G. volans* removal, apparently preempting a response by the subordinate *P. borealis*.

I also found support for the hypothesis that rat snakes (*Elaphe* spp.) indirectly enhance cavity availability for *P. borealis* by preying differentially on kleptoparasites. Differential predation was predicted because *P. borealis*, but not kleptoparasites, maintain anti-snake resin barriers around their cavities. Daily nest survival rates were similar among *P. borealis*, *M. carolinus*, and great crested-flycatchers (*Myiarchus crinitis*) during incubation, but highest for *P. borealis* (i.e., *P. borealis* >> *M. carolinus* = *M. crinitis*) during the nestling stage, when snake predation is most frequent.

Markov models of cavity occupancy-dynamics, parameterized with field data, effectively captured aspects of the community outlined above. Moreover, annual Markov models showed that *P. borealis* breeding males, whose cavity is used for nesting, shunned cavities that were vacant or occupied by kleptoparasites the previous year, whereas breeding females and helpers frequently occupied such cavities. Another application of Markov models revealed that *M. carolinus*'s response to squirrel removal resulted largely from a >10-fold increase in rates of transition from *G. volans* to *M.*

carolinus, indicating rapid colonization by *M. carolinus* of cavities from which squirrels were removed.

CHAPTER 1 GENERAL INTRODUCTION

In this study I combine observational/comparative, experimental, and mathematical-modeling approaches to examine the effects of heterospecific cavity occupation (cavity kleptoparasitism) on the endangered red-cockaded woodpecker (*Picoides borealis*), a cooperative breeder. I also evaluate the potential importance and consequences of indirect effects among *P. borealis* and its two primary kleptoparasites, red-bellied woodpeckers (*Melanerpes carolinus*) and southern flying squirrels (*Glaucomys volans*). In addition, I examine the potential mediating effects of a shared predator, rat snakes (*Elaphe spp.*), on interactions between *P. borealis* and kleptoparasites. Field work was conducted at two forests in northern peninsular Florida: Camp Blanding Training Site (CBTS) and Goethe State Forest (GSF).

I present the research in a series of four separate papers (Chapters 2-5). I first evaluate the hypotheses that (1) *P. borealis* group size, an index of group fitness, is cavity limited, and (2) heterospecific occupants (cavity kleptoparasites) exacerbate this limitation, by examining simple and partial correlations among these variables (Chapter 2). Based on certain findings presented in Chapter 2, I proposed the following dominance hierarchy among the primary occupants of *P. borealis* cavities: *G. volans* > *M. carolinus* > *P. borealis*. This hypothesis, the focus of Chapter 3, was tested at CBTS in a *G. volans* removal experiment that used a before-after control-removal design. In Chapter 4, I evaluate the hypothesis that rat snakes (*Elaphe spp.*) indirectly enhance

cavity availability for *P. borealis* by preying differentially on kleptoparasites.

Differential predation was predicted because *P. borealis*, but not kleptoparasites, maintain anti-snake resin barriers around their roost and nest cavities. I evaluated this hypothesis by comparing the daily survival rates of *P. borealis*, *M. carolinus*, and great crested-flycatchers (*Myiarchus crinitus*). In Chapter 5, I use Markov chain models well parameterized with field data to examine in detail the structural dynamics of the study community, and to further explore the hypotheses considered in previous chapters.

Chapter 6 provides a summary of the study's conclusions.

CHAPTER 2
CAVITY NUMBER AND HETERSPECIFIC CAVITY OCCUPATION
AS CORRELATES OF GROUP SIZE IN RED-COCKADED WOODPECKERS

Introduction

Nest site limitation is well documented for non-excavating cavity-nesting birds, many of which are amenable to nest-box studies (Newton 1994a,b). Woodpeckers (picidae) and other excavators are presumed to be less cavity-limited (Wesolowski 1983, Martin 1993). Nonetheless, cavities are critical to woodpeckers for roosting (survival) and nesting (reproduction). As such, factors that influence their availability on a territory will directly or indirectly affect fitness (Short 1979, Martin 1986). The foremost of such factors is the density of suitable excavation sites, which varies widely across habitats (Conner et al. 1976, Raphael and White 1984, Wesolowski and Tomialojc 1986, Horton and Mannan 1988, Welsh and Capen 1992, Schepps et al. 1999, Jackson and Jackson 2004). Pairs on territories that are poor in excavation sites may struggle to meet their roosting and nesting requirements.

Additionally, most woodpecker species require individual roost cavities. Breeding males, which are dominant over females, typically roost in the nest cavity (Short 1979, Winkler et al. 1995). Females and juveniles roost in former nest cavities or holes excavated specifically for roosting (Short 1979, Bull 1987, Bull et al. 1992, Aubry and Raley 2002). Cavity shortages cause some individuals to roost outside, where they may be more vulnerable to predators and inclement weather (Kendeigh 1961, Harris and Jerauld 1982, Hooper and Lennartz 1983, Carter et al. 1989). Thus, males on

cavity-limited territories may incur fitness costs through reduced survival of juveniles and breeding females, and from mate dispersal (Short 1979, Daniels and Walters 2000).

The usurpation and occupation of cavities by non-excavators, which are largely dependent on woodpecker cavities (Short 1979, Van Balen et al. 1982, Sedgwick and Knopf 1992, McClelland and McClelland 2000, Martin et al. 2004, Saab et al. 2004), may exacerbate preexisting limitation or cause such conditions to emerge. Although non-excavators benefit (+) from this interaction (Martin and Eadie 1999), the phenomenon is generally referred to as interspecific competition (Short 1979, Martin et al. 2004), even though the interaction is not reciprocally negative (-,-), or even asymmetrical (0,-), as is required by definition (Macarthur 1972, Lawton and Hassell 1981, Connell 1983, Wiens 1989). Instead, the interactions constitutes either commensalism (0,+) or kleptoparasitism (-,+; Kappes 1997), depending upon the outcome for woodpecker pairs. If optimal back-up cavities are available on a territory, older cavities can be occupied by other species without fitness costs to the excavator. Otherwise, heterospecific usurpation or preemptive occupation of nest or roost sites may reduce survival, pair-bond stability, reproductive success, and re-nesting potential (Short 1979, Kerpez and Smith 1990, Ingold 1994, Glue and Boswell 1994, Labranche and Walters 1994, Walters and Miller 2001, Kappes 1997, Kappes 2004).

In short, the quality of an excavator territory (as defined by survival and nesting success) is determined in large measure by cavity availability (Kilham 1961, Short 1979, Kerpez and Smith 1990, Ingold 1994, Kappes and Harris 1995, Sedgwick 1997). Cavity availability in turn is a function of cavity number and the rate of heterospecific occupation. In the case of cooperatively breeding cavity nesters, cavity availability may

limit family-group fitness. I monitored red-cockaded woodpecker (*Picoides borealis*) group size (an index of group fitness—see below), cavity number, and the rate of heterospecific occupancy at two Forests from 1997 to 2001, in order to assess the relationships between group size and measures of cavity availability. In particular, I used correlation analyses to evaluate the hypotheses that (1) cavity number may limit *P. borealis* group size, and (2) cavity occupation by heterospecifics can cause or exacerbate this limitation.

The Study System

Picoides borealis is a federally endangered cooperative breeder endemic to the fire-maintained pine forests of southeastern North America. Family groups consist of a single breeding pair and 0-3 helpers (Walters 1990). The availability of cavities, which are excavated in living pines, and used for nesting and year-round for roosting, is the primary determinant of territory quality (Ligon 1970, Copeyon et al. 1991, Walters et al. 1992a, Davenport et al 2000, USFWS 2003). Cavities require one to several years to excavate but remain suitable for many years. Sets of cavity trees, termed clusters (Walters 1990), are typically aggregated within a group's territory. The most recently completed cavity usually becomes the breeding male's roost (Conner et al. 1998). Breeding females, helpers, and juveniles roost in older cavities, including former nest holes, and are less likely to remain on cavity-limited territories (Doerr et al. 1989, Carrie et al. 1998, Daniels and Walters 2000, Kappes 2004). Thus, group size and stability can be cavity limited (Carrie et al. 1998).

Picoides borealis constructs a resin barrier that deters rat snakes (*Elaphe* spp.); Dennis 1971a, Jackson 1974; Rudolph et al. 1990a). The resin barrier is maintained only

around "active" cavities, i.e., those in current use by *P. borealis* (Jackson 1977). Even after several years of inactivity and/or occupation by other species, a cavity can be reactivated by *P. borealis* unless the cavity tree dies or the cavity becomes too enlarged (Baker 1971, Jackson 1978, Doerr et al. 1989, Walters 1990).

Numerous species of cavity nesters commonly occupy *P. borealis* cavities. Although most of these species tend to occupy abandoned or excess cavities, red-bellied woodpeckers (*Melanerpes carolinus*) and southern flying squirrels (*Glaucomys volans*) can exacerbate cavity limitation by usurping and occupying cavities (Dennis 1971b, Jackson 1978, Rudolph et al. 1990b, Loeb 1993, Kappes and Harris 1995, Kappes 1997, Kappes 2004). To date, studies of the effects of heterospecific cavity occupation on *P. borealis* have focused on the nesting success of groups containing a breeding pair (Conner et al. 1996, Laves and Loeb 1999, Mitchell et al. 1999). I focus on the question of whether heterospecific occupation of *P. borealis* cavities exacerbates cavity limitation of group size.

Group Size as a Response Variable

Territorial males constitute the core of the *P. borealis* social unit. Whereas breeding females and helpers commonly disperse between breeding seasons, breeding males normally remain on their territory for life (Walters et al. 1988). Solitary birds are typically males who have either lost their mate or colonized an inactive cluster (Walters 1990). Obviously, solitary males suffer lower reproductive success, but they also experience lower survival (Walters et al. 1988). When a solitary male acquires a mate, this signifies an increase in the group's (predicted) fitness. Helper retention further increases the survival and reproductive success of breeders (Lennartz et al. 1987, Walters

1990, Khan and Walters 2002). Helpers gain current, future, direct and indirect fitness by helping (Walters et al. 1988, Walters et al. 1992b, Khan and Walters 2002). In short, the survival and reproductive success of *P. borealis* group-members increases directly with group size. Therefore, group size is a suitable metric of habitat quality (Li and Martin 1991, Carrie et al. 1998, Davenport et al. 2000, USFWS 2003).

Methods

Study Areas

Work was conducted at two Forests in northern peninsular Florida: Camp Blanding Training Site (CBTS) in Clay County, and Goethe State Forest (GSF) in Levy County, where approximately 16 and 30 *P. borealis* groups occur, respectively. All clusters occurred in open, mature longleaf pine (*Pinus palustris*) forest with an understory dominated by saw palmetto (*Serenoa repens*) and wiregrass (*Aristida stricta*). Prescribed fires were conducted at 3-5 year intervals in the study clusters and surrounding forest. At CBTS, group size, cavity number, and cavity occupancy were monitored in 13 to 16 clusters per year from 1997 to 2001 (total = 72 cluster-years). At GSF, 15 to 17 clusters were monitored between 1998 and 2001 (total = 66 cluster-years). Within these study clusters, I only monitored suitable cavities, as defined by entrance diameter < 60 mm and occurrence in living trees (Kappes and Harris 1995, Rudolph et al. 1990b). All of the study clusters were surrounded by sufficient foraging habitat to support a *P. borealis* group (USFWS 2003). *Picoides borealis* occupied each of the study clusters at some point during the study. I continued to monitor clusters that were abandoned or occupied by single males.

Cavity Monitoring

Cavity clusters were censused 7-9 times per breeding season (April to July), at 10-14 day intervals using a combination of day-time inspections, night-time inspections, and roost checks. At each census interval, I initially inspected each cavity during the day using ladders, a drop-light and mirror, or a video camera mounted on a telescoping pole (TreeTop Peeper, Sandpiper Technologies, Inc., Manteca, California). I also noted the presence or absence of resin-well maintenance by *P. borealis*. If a cavity was empty, but exhibited abundant evidence of fresh *P. borealis* resin-well work, I assumed it was occupied by *P. borealis* at that census interval. If the cavity contained *G. volans* (a nocturnal species), avian eggs or nestlings, or some other taxon, I recorded the appropriate species as the occupant at that census. If the cavity was empty but exhibited no evidence of current resin-well maintenance, I returned that night and checked for roosting birds using an infra-red option on the video camera. Typically, night-time inspections would reveal either an empty cavity or a roosting *M. carolinus*. If the cavity was empty during the day-time check and exhibited marginal evidence of *P. borealis* activity, or if the resin-well status had changed since the previous census, the cavity was re-visited for a pre-sunset roost check in which an observer watched the cavity to determine if any birds entered it to roost. Roost checks enabled me to determine a cavity's occupancy status without disturbing any birds that had only recently colonized a particular hole. For each cluster, I calculated the mean number of cavities occupied by each species as the average across the 7-9 censuses. Throughout this dissertation, unless otherwise stated, a species' *occupancy* is the mean number of *P. borealis* cavities in a

cluster-year that were occupied by that species; and *cavities* refer specifically to *P. borealis* cavities.

General Data Analysis

To compare the composition of the communities occupying *P. borealis* cavities at the two study sites, I only used data from 1998 to 2001, since data from 1997 were lacking for GSF. Correlation analysis was used to evaluate the relationships between group size and: 1) cavity number, 2) *M. carolinus* occupancy, 3) *G. volans* occupancy, and 4) total heterospecific occupancy.

Because of small yearly sample sizes or inherent skewness of the data, the variables were rarely normally distributed and various transformations failed to remedy this problem. Therefore, Spearman's rank methods were used to calculate both simple (bivariate) and partial correlations (Shipley 2000). Based on the *a priori* predictions that group size would increase with increasing cavity number and decrease with increasing levels of heterospecific occupancy, one-tailed tests were used.

Results

Community Compositions

The annual mean for *P. borealis* group size at CBTS and GSF averaged 2.26 (range = 2.13 to 2.46) and 2.31 (range = 2.18 to 2.41), respectively (Figure 2-1). The annual, mean number of suitable cavities per cluster averaged 5.13 (range = 4.88 to 5.46) at CBTS and 4.35 (range = 4.20 to 4.47) at GSF. Thus, whereas mean group size was similar at the two forests, the mean number of cavities was consistently higher at CBTS (Figure 2-1).

Annual mean occupancy by *M. carolinus* averaged 0.73 (range = 0.63-0.82) cavities per cluster at CBTS and 0.77 (range = 0.66-0.84) at GSF (Figure 2-2). Annual mean occupancy by *G. volans* at CBTS and GSF averaged 0.87 (range = 0.6-1.03) and 0.28 (range = 0.15-0.38) cavities per cluster, respectively. The annual mean number of cavities per cluster that were occupied by passerines [great-crested flycatcher (*Myiarchus crinitus*), tufted titmouse (*Parus bicolor*), and Eastern bluebirds (*Sialia sialis*)], were similar at the two sites, averaging 0.10 (range = 0.05-0.13) cavities per cluster at CBTS and 0.12 (range = 0.07-0.17) at GSF. Because of the small number of cavities occupied by passerines at both sites, this group was excluded from further analyses except for its inclusion in total heterospecific occupancy. Total heterospecific occupancy averaged 1.75 (range = 1.62-1.84) cavities per cluster at CBTS and 1.19 (range = 1.12-1.31) at GSF (Figure 2-3).

In summary, whereas cavity occupancy by *M. carolinus* and passerines was similar at the two sites, *G. volans* occupancy averaged 3.11 times greater (range = 2.3-6.9 fold) at CBTS than at GSF. Total heterospecific occupancy at CBTS averaged 1.47 times greater (range = 1.40-1.53 fold) than at GSF (Figure 1C), due to the greater occupancy by squirrels. At both sites, total heterospecific occupancy exhibited less annual variation than either of the two primary heterospecific occupants (Table 2-1).

Correlation Between Group Size and Cavity Number

Group size and cavity number were positively correlated in all five years at CBTS. This relationship was highly statistically significant in 2000 and 2001 but non-significant in the first three years (Table 2-2). Group size and cavity number were unrelated at GSF (Table 2-2). However, raw cavity number provides an inaccurate

measure of actual cavity availability because of high rates of heterospecific occupancy.

At CBTS, controlling for heterospecific occupation substantially increased the correlation between cavity number and group size in all years except 1999, and the relationship became highly statistically significant in all years except 1999 (Table 2-3). At GSF, the strength of the relationship increased and became positive in all four years, becoming highly statistically significant in 1998 and marginally statistically significant in 2000 (Table 2-3).

Correlations between Group Size and Heterospecific Occupancy

Variation in cavity number obfuscates the relationship between group size and heterospecific cavity occupancy. Therefore, I calculated the partial correlations, controlling for cavity number. At CBTS, the partial correlations between group size and *M. carolinus* occupancy indicated an inconsistent or even contradictory pattern of association between these two variables (Table 2-4). The partial correlation between *G. volans* occupancy and group size, however, was negative in all five years, being at least marginally statistically significant in four of the five years and highly significant in 1999 and 2001. Partial correlations between group size and total heterospecific occupancy at CBTS revealed a highly statistically significant negative relationship in all years except 1999, when the partial correlation between group size and *M. carolinus* occupancy was strongly positive (Table 2-4).

At GSF, the partial correlations between group size and *M. carolinus* occupancy were negative in all four years, but statistically significant only in 1999 (Table 2-5). No relationship between group size and *G. volans* occupancy was evident. The partial correlations between group size and total heterospecific occupancy, however, were

negative in all four years, being highly statistically significant in 1998 and 2000, and statistically significant in 1999 (Table 2-5).

Potential Higher Order Interactions

Although the partial correlations between group size and total heterospecific occupancy were consistently and statistically significantly negative at both forests, those between group size and the two primary species of heterospecific occupants differed between forests (Tables 2-4 and 2-5). At CBTS, where squirrels were a frequent cavity occupant, group size was consistently negatively correlated with *G. volans* occupancy, but erratically associated with *M. carolinus*. At GSF, where squirrels were less important occupants, but *M. carolinus* occupancy was similar to CBTS, group size was uncorrelated with squirrels and consistently negatively associated with *M. carolinus*. I hypothesized that the relationship between group size and *M. carolinus* occupancy changed between forests because of a higher-order interaction (Wootton 1994) involving *G. volans*. That is, the relationship between group size and *M. carolinus* occupancy depended on the level of squirrel occupancy. I evaluated this hypothesis by calculating for both forests the partial correlation between group size and *M. carolinus* occupancy, controlling for both cavity number and squirrel occupancy. I predicted that the relationship between group size and *M. carolinus* would be more negative when controlling for both cavity number and squirrel occupancy than when controlling only for cavity number (i.e., in comparison to Tables 2-4 and 2-5). Moreover, the negative relationship should increase for both forests but more so for CBTS, where the influence of *G. volans* was greater. These predictions were supported by the results (Table 2-6). At CBTS, the negative relationship increased notably, and the sign of the correlation coefficient became

negative, in all five years. Moreover, these partial correlations between group size and *M. carolinus* occupancy became highly statistically significant in 1997, and marginally statistically significant in 2000 and 2001. Similarly, at GSF, controlling for both cavity number and squirrel occupancy increased the negative correlations between *M. carolinus* and group size, although this increase was less dramatic. Nonetheless, the GSF partial correlations became highly statistically significant in 1999 and 2000, and marginally significant in 1998 (Table 2-6).

Discussion

The primary hypotheses of this paper were (1) that *P. borealis* group size is cavity-limited, and (2) that heterospecific occupants can cause or exacerbate this limitation. Hypothesis 1 was first evaluated by analyzing the simple correlations between group size and raw cavity number. Results indicated a positive, but statistically inconsistent relationship between group size and cavity number at CBTS, and no relationship at GSF (Table 2-2). However, raw cavity number provided a poor estimate of cavity availability because other species occupied an average of 1.75 (34%) of the cavities per cluster at CBTS and 1.19 (27%) at GSF. By accounting for heterospecific occupation, the correlations between group size and cavity number were increased substantially in the positive direction for both forests (Table 2-3). At CBTS, the relationship became highly statistically significant in four of the five years. At GSF, the relationship became positive in all four years, and statistically significant in two of these years. Overall, these results support the hypothesis that group size is limited by cavity availability, as estimated by accounting for heterospecific occupancy (Figure 2-2).

Group Size and Heterospecific Occupancy

The partial correlations between group size and total heterospecific occupancy, controlling for cavity number, were consistently negative and statistically significant at both forests. These results strongly support the hypothesis that heterospecific occupation of *P. borealis* cavities can cause or exacerbate cavity limitation of group size. However, the primary species driving this relationship changed between forests with the level of occupancy by *G. volans*, suggesting that this species was the dominant interactor. Squirrels are apparently dominant over both species of woodpecker and *M. carolinus* is dominant over *P. borealis* (Figure 2-4). Where *G. volans* occupancy is relatively high (e.g., CBTS), it suppresses both group size and *M. carolinus* occupancy, thereby obscuring the relationship between the two woodpecker species (or even causing them to appear mutualistic; Table 2-4, 1999). Thus, *G. volans* imparts both a negative direct effect and a positive indirect effect on group size (Lawlor 1979; Figure 2-4). As a result, the negative effect of *M. carolinus* on group size was manifested only where squirrel occupancy was low, as at GSF; or when squirrel occupancy was statistically controlled, as was required for the CBTS data.

Further evidence of a consequential interaction between squirrels and *M. carolinus* is that the annual variation in mean occupancy by both species is greater than that of total heterospecific occupancy (Figure 2-1, Table 2-1). Given the conclusions outlined in the previous paragraph, this pattern might result from occupancy compensation by *M. carolinus* in response to variation in occupancy by the dominant interactor, *G. volans*. I evaluated this explanation further by plotting the annual mean occupancies of *M. carolinus* against those of *G. volans* using data from CBTS, where

both species were well represented. Annual mean *M. carolinus* occupancy was strongly negatively correlated with squirrel occupancy (Figure 2-3). Combined with the observed forest-to-forest change in the relationship between *M. carolinus* and group size with the level of *G. volans* occupancy, I suspect that *G. volans*, not *M. carolinus*, is driving this relationship. That is, *M. carolinus* occupancy compensates according to *G. volans* occupancy, resulting in a relatively constant total heterospecific occupancy.

Evaluating Additional Influential Factors

Simple and partial correlations tended to be weaker at GSF than at CBTS (Tables 2-2 to 2-6). One possible explanation for this pattern was a higher rate of cavity tree mortality at GSF (unpublished data), which may have precluded group size from tracking cavity number and availability at this forest. Another factor that may have weakened the GSF correlations was a lack of variation in group size compared to CBTS (Figure 2-1). At GSF, over 98% of the 66 cluster-years involved groups composed of two or three individuals. At CBTS, 76% of the cluster-years involved groups of two or three individuals, 15% involved zero or one individual, and 8% involved four or five individuals.

Also, in addition to cavity availability, unmeasured components of territory quality must account for much of the variation in group size. The most important of these factors is recurrent fire, which improves the quality of foraging habitat; thereby enhancing group formation, stability and size (James et al. 1997, USFWS 2003, Kappes et al. 2004). Moreover, members of groups in high-quality foraging habitat may be in better physical condition. This may enable them to better survive bouts of roosting

outside (Williams et al. 1991), thereby improving maintenance of group size even in cavity-limited clusters.

Nonetheless, certain aspects of *P. borealis* ecology may predispose it to cavity limitation and heterospecific exacerbation of this limitation. The slow supply rate of cavities is often exceeded by rates of loss to tree mortality, enlargement, and heterospecific usurpation, resulting in cavity shortages (Walters 1991). Moreover, recurrent fire can decimate the substrates used by other excavators for cavity construction (Ligon 1970, Kappes and Harris 1995). As a result, *P. borealis* cavities constitute a disproportionate number of the sites available to other cavity nesters.

Finally, as with any correlative study, conclusions must be drawn with caution. For example, variation in group size may have caused variation in heterospecific occupation. This latter scenario seems unlikely, however, given that usurpations of active *P. borealis* cavities by both *G. volans* and *M. carolinus* were frequently observed during this study, whereas the reverse was not. Thus, I suspect that the negative correlations between group size and heterospecific occupancy were driven by the latter. Nonetheless, a removal experiment is needed to test this interpretation (Chapter 3).

Table 2-1. Coefficients of variation of the occupancy rates of *M. carolinus*, *G. volans*, and all heterospecific cavity occupants combined at CBTS and GSF.

Ecological state	CBTS	GSF
<i>M. carolinus</i>	0.116	0.099
<i>G. volans</i>	0.223	0.401
All heterospecifics	0.054	0.070

Table 2-2. Simple Spearman rank correlations (sample sizes in parentheses) between *P. borealis* group size and total number of suitable cavities at CBTS and GSF, 1997 to 2001.

	1997 (14)	1998 (13)	1999 (13)	2000 (16)	2001 (16)
CBTS	0.279	0.179	0.363	0.514***	0.558***
GSF	No data	0.335	0.000	0.121	0.000

1-tailed test, *0.10 > P > 0.05, **0.05 > P > 0.03, ***P < 0.03.

Table 2-3. Spearman rank partial correlations between *P. borealis* group size and the number of cavities, controlling for heterospecific occupancy.

Year	Site	
	Camp Blanding	Goethe State Forest
1997	0.655***	No data
1998	0.624***	0.627***
1999	0.027	0.253
2000	0.681***	0.411*
2001	0.786***	0.143

1-tailed test, *0.10 > P > 0.05, **0.05 > P > 0.03, ***P < 0.03.

Table 2-4. Yearly (sample size in parentheses) Spearman rank partial correlations between *P. borealis* group size and the mean number of cavities occupied by *M. carolinus*, *G. volans*, and all heterospecifics combined at CBTS, controlling for the total number of cavities.

	1997 (14)	1998 (13)	1999 (13)	2000 (16)	2001 (16)
<i>M. carolinus</i>	-0.391*	-0.317	0.504**	0.034	0.042
<i>G. volans</i>	-0.421*	-0.270	-0.695***	-0.414*	-0.676***
All heterospecifics	-0.619***	-0.632***	0.231	-0.529***	-0.673***

1-tailed test, *0.10 > P > 0.05, **0.05 > P > 0.03, ***P < 0.03

Table 2-5. Yearly (sample size in parentheses) Spearman rank partial correlations between *P. borealis* group size and the mean number of cavities occupied by *M. carolinus*, *G. volans*, and all heterospecifics combined at GSF, controlling for the total number of cavities.

	1998 (15)	1999 (17)	2000 (17)	2001 (17)
<i>M. carolinus</i>	-0.352	-0.722***	-0.138	-0.294
<i>G. volans</i>	-0.299	0.016	-0.308	0.222
All heterospecifics	-0.615***	-0.437**	-0.564***	-0.231

1-tailed test, *0.10 > P > 0.05, **0.05 > P > 0.03, ***P < 0.03.

Table 2-6. Spearman rank partial correlations between *P. borealis* group size and the number of cavities occupied by *M. carolinus*, controlling for both cavity number and *G. volans* occupancy.

Year	Site	
	Camp Blanding	Goethe State Forest
1997	-0.602***	No data
1998	-0.338	-0.409*
1999	-0.006	-0.741***
2000	-0.391*	-0.547***
2001	-0.378*	-0.214

1-tailed test, *0.10 > P > 0.05, **0.05 > P > 0.03, ***P < 0.03.

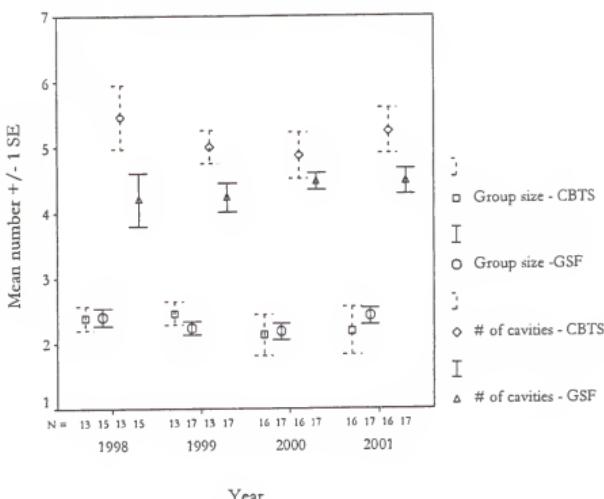


Figure 2-1. Annual means (± 1 SE) for group size and the number of cavities per cluster, Camp Blanding Training Site (CBTS) and Goethe State Forest (GSF).

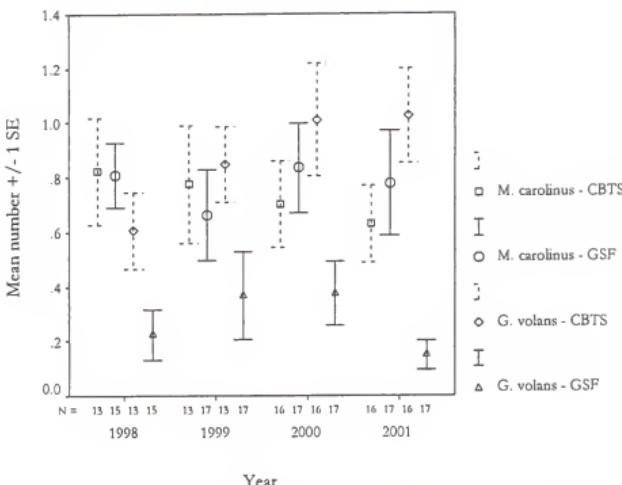


Figure 2-2. Annual means (+/- 1 SE) for the mean number of cavities per cluster occupied by *M. carolinus* and *G. volans* at CBTS and GSF.

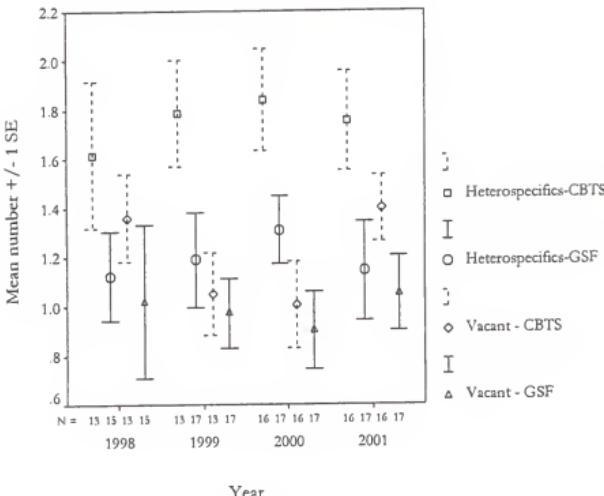


Figure 2-3. Annual means (\pm one standard error) for the mean number of cavities per cluster which were occupied by heterospecifics and the mean number of cavities per cluster which were vacant, at Camp Blanding Training Site (CBTS) and Goethe State Forest (GSF).

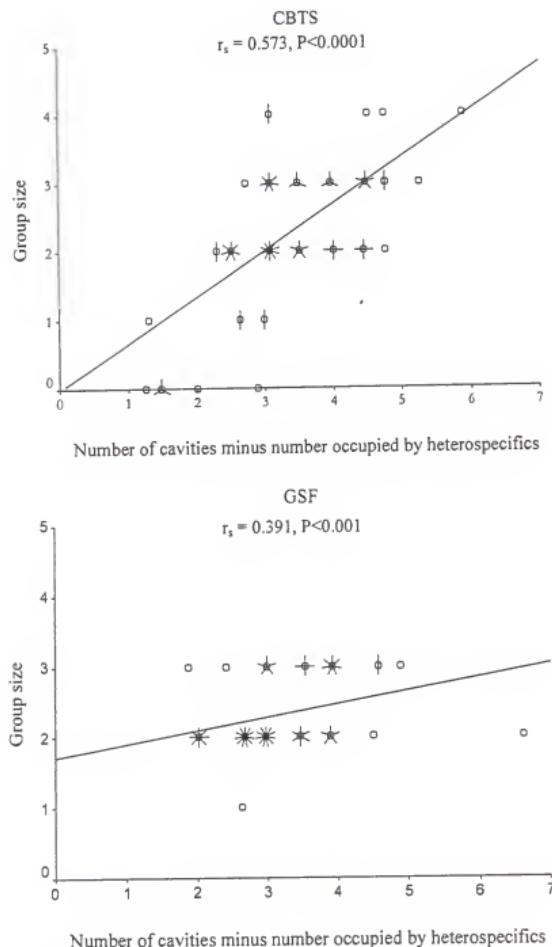


Figure 2-4. *Picoides borealis* group size in relation to cavity availability at CBTS (top) and GSF (bottom). Cavity availability in a particular cluster and year was calculated as the number of suitable cavities, minus the mean number of cavities that were occupied by heterospecifics. Circles indicate single data points. Circles with petals indicate multiple data points, one petal per data point. CBTS data are from 13-16 clusters per year, 1997-2001 (72 cluster-years). GSF data are from 15-17 clusters per year, 1998-2001 (66 cluster-years).

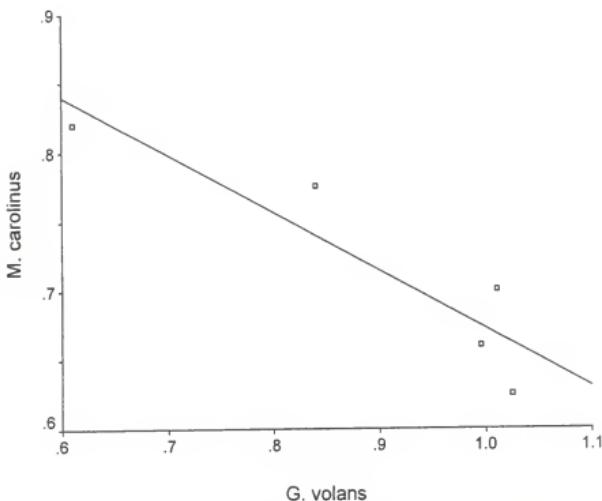


Figure 2-5. Plot of the annual mean number of cavities per cluster occupied by *M. carolinus*, against the annual mean number of cavities per cluster occupied by *G. volans*. Data are from CBTS, 1997-2001 ($r_s = 0.900$, $P = 0.037$, $n = 5$ years).

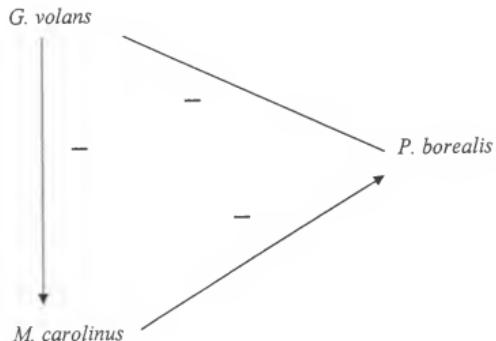


Figure 2-6. Proposed community interaction web for the three most frequent occupants of *P. borealis* cavities. *G. volans* is dominant over *M. carolinus* and *P. borealis*. *Melanerpes carolinus*, in turn, is dominant over *P. borealis*.

CHAPTER 3
EFFECTS OF SOUTHERN FLYING SQUIRRELS (*Glaucomys volans*)
ON THE OCCUPATION OF RED-COCKADED WOODPECKER
(*Picoides borealis*) CAVITIES: A REMOVAL EXPERIMENT

Introduction

The alteration of ecosystems by humans has lead to an overabundance of opportunistic native species that may prey upon, compete with, or parasitize more ecologically vulnerable species (Sweitzer et al. 1996). In response, biologists have established removal programs that aim to reduce the negative effects of such interactions on sensitive or endangered species (e.g., Wanless et al. 1996, Smith et al. 2002). However, several issues emerge regarding the implementation of such programs (Garrot et al. 1993, Goodrich and Buskirk 1995). First, removal activities may present managers with moral and fiscal dilemmas. Also, control measures may not achieve the desired results in all locales because of spatial variation in the strength of interactions between particular species (Robinson et al. 1993, Menge et al. 1994). Finally, such efforts may lead to unexpected consequences stemming from poorly understood indirect effects (Wootton 1994). These considerations point to the need for experimental evaluation of the efficacy of species removal programs (Robinson et al. 1993, Hall and Rothstein 1999, Mitchell et al. 1999, Henke et al. 1999).

Southern flying squirrels (*Glaucomys volans*) are significant predators of the nests of cavity nesting birds (Stabb et al. 1989, Albano 1992, Miller 2002, Chapter 3), including the endangered, cooperatively breeding red-cockaded woodpecker (*Picoides*

borealis), of which *G. volans* is also an important cavity kleptoparasite (Loeb 1993, Kappes 1997, Chapter 2). As such, *G. volans* removal has become a standard practice in *P. borealis* management (Richardson and Stockie 1995, Montague et al. 1995, Gaines et al. 1995, USFWS 2003). However, only two studies (Laves and Loeb 1996, Mitchell et al. 1999) have experimentally evaluated the effectiveness of such programs, and both of these restricted their investigations to the effects of *G. volans* on the nesting success of *P. borealis* groups containing at least a breeding pair. The effects of *G. volans* on actual cavity occupancy by *P. borealis* has not been studied experimentally. Moreover, *P. borealis* uses cavities year-round for roosting. Thus *G. volans* kleptoparasitism may have consequences not limited to the breeding season. In this paper I address the effects of *G. volans* on cavity occupancy by *P. borealis* throughout the year.

Another issue is that researchers have oversimplified the community associated with *P. borealis* cavities by focusing on pair-wise interactions between squirrels and *P. borealis* (Loeb 1993, Laves and Loeb 1996, Conner et al. 1996, Mitchell et al. 1999). Given that multiple species use these cavities in any particular forest, the potential exists for higher-order interactions, which may lead to unanticipated consequences of *G. volans* (squirrel) removal. For example, my work has shown that both *G. volans* and red-bellied woodpeckers (*Melanerpes carolinus*) were important cavity kleptoparasites of *P. borealis* (Chapter 1), but their relative rates of cavity occupancy varied dramatically between forests. *Melanerpes carolinus* occupancy was similar at the two study sites (~ 0.75 cavities per cluster), but *G. volans* occupancy was over three times higher at Camp Blanding Training Site (CBTS) than at Goethe State Forest (GSF; 0.87 vs. 0.28). Correspondingly, where *G. volans* occupancy was high (CBTS), group size was

bivariately uncorrelated with *M. carolinus* occupancy, but strongly negatively associated with *G. volans* occupancy. However, the partial correlations between group size and *M. carolinus* were negative. Moreover, where squirrels were less frequent cavity occupants (GSF), *P. borealis* group size was negatively associated with *M. carolinus* and uncorrelated with squirrels. Based on this pattern, I proposed the following transitive dominance hierarchy: *G. volans* > *M. carolinus* > *P. borealis* (Chapter 1, see also Buss and Jackson 1979).

In this study, I tested the above interpretation of the dominance hierarchy by conducting a flying squirrel removal experiment at CBTS. Using a paired before-after experimental design, I compared the occupancies of *P. borealis*, *M. carolinus*, and *G. volans* on eight control plots and eight treatment plots where I removed *G. volans* from *P. borealis* cavities. I predicted that *M. carolinus* occupancy of *P. borealis* cavities would increase in clusters where squirrels were removed (competitive release). Given the proposed structure of the dominance hierarchy, I also predicted that this increase in *M. carolinus* occupancy would at least partially preempt a positive occupancy-response by *P. borealis*, resulting in a weakly positive or neutral response by the endangered woodpecker.

Methods

Study Area

Work was conducted in northern peninsular Florida at Camp Blanding Training Site (CBTS) in Clay County. In April 2000, sixteen cavity-tree clusters, constituting nearly all of the *P. borealis*-suitable clusters at CBTS (Kappes et al. 2004), were selected to study the effects of *G. volans* on the occupancy of *P. borealis* cavities. Each cluster

occurred in open, mature longleaf pine (*Pinus palustris*) forest with an understory dominated by saw palmetto (*Serenoa repens*) and wiregrass (*Aristida stricta*). Prescribed fires were conducted at 3-5 year intervals at both Forests prior to the study. All 16 clusters were surrounded by sufficient foraging habitat to support a *P. borealis* group (USFWS 2003) and each was occupied by this species at some point during the study. I continued to monitor clusters that were abandoned by *P. borealis* or occupied by solitary birds. The number of cavities per study-cluster ranged from three to seven (mean = 5.06; Chapter 2).

Field Work

Data were collected over 27 months, April 2000 to June 2002. However, the initial three-month period (April-June 2000) was excluded from formal analysis. Formal analysis was restricted to the last 24 months, which were divided into two, 12-month phases. The first phase (July 2000-June 2001) was a pre-removal (Before) phase, at the end of which the 16 clusters were paired according to their similarity with respect to the mean proportion of cavities occupied by *G. volans* during April-May of 2001. Members of each cluster pair were randomly designated as a control or removal based on a coin toss. During the second (After) phase, the subsequent 12-month time-interval (July 2001-June 2002), any *G. volans* encountered within the removal clusters during routine inspections (see below) were pulled from the cavity using mechanical fingers and euthanized (IACUC citation).

Throughout the study, the occupancy of all *P. borealis*-suitable cavities within the 16 study clusters was monitored at 10-14 day intervals using a combination of day-time and night-time inspections, and roost checks. Suitable cavities were defined by

occurrence in living trees and an entrance diameter of < 60 mm (Kappes and Harris 1995, Rudolph et al. 1990b). At each census interval, I initially inspected each cavity during the day using ladders, a drop-light and mirror, or, a video camera mounted on a telescoping pole (TreeTop Peeper, Sandpiper Technologies, Inc., Manteca, California). I also noted the presence or absence of resin-well maintenance by *P. borealis*. If the cavity was empty, but exhibited abundant evidence of fresh resin-well work, I assumed the cavity was occupied by *P. borealis* at that census interval. If the cavity contained *G. volans* (a nocturnal species), avian eggs or nestlings, or any other taxon, I recorded the appropriate species as the occupant. If the cavity was empty and exhibited no evidence of current resin-well maintenance, it was re-visited that night and checked for roosting birds using an infra-red option on the video camera. Night inspections would usually reveal either an empty cavity or a roosting *M. carolinus*. If the cavity was empty during the day-time inspection and exhibited marginal evidence of resin-well maintenance by *P. borealis*, or if the resin-well status had changed since the previous census, the cavity was re-visited for a pre-sunset roost check in which I watched the cavity to determine if any birds entered it to roost. Roost checks enabled me to determine a cavity's occupancy status without disturbing any bird that may have recently colonized the cavity.

Calculation of Occupancy Rates

For each cluster, I calculated the mean number of cavities occupied by each species (i.e., its occupancy), as the average across censuses conducted *within* designated sampling periods (see below). The vacancy rate for each cluster was calculated the same way. Throughout this paper, unless otherwise stated, a species' *occupancy* refers to the

mean number of *P. borealis* cavities per cluster that were occupied by that species during the designated time period, and *cavities* refer specifically to *P. borealis* cavities.

The 27 months of occupancy data were organized into nine, three-month time periods (seasons) for analysis. A 24-month subset of the data was used to develop a one-year before-after data set, which was used to compare the occupancy of each species during July 2000-June 2001 of the Before phase to July 2001-June 2002 of the After phase (note that April-June 2000 was excluded to balance the data at 12 months Before and 12 months After). For each cluster, the mean occupancy of each species was calculated for each 12-month period as follows. The 30 or so censuses conducted within the 12-month period were sub-divided into the period (season) in which they occurred: summer (July-September), fall (October-December), winter (January-March), and Spring (April-June). Then, for each cluster, the mean occupancy of each species was then calculated across the 7-9 censuses conducted within that season using:

$$\text{Cavity occupancy} = \sum x_i / I C \quad (3-1)$$

where x_i is the number of cavities occupied by that species during census i ($i = 1 \dots I$), I is the total number of censuses conducted within the cluster during that season, and C is the number of cavities in the cluster. The vacancy rate was calculated the same way.

Finally, separate mean occupancies were then calculated, for the Before and Removal phases, as the mean across the four seasons (mean of means) within each 12-month phase.

Comparing Occupancies in the Control and Removal Clusters

For each species, I compared its mean occupancy, as calculated using equation 1, during the 12-month Before and Removal phases using paired t-tests in which the cluster

pairs ($n = 8$) were the experimental units. The paired t-tests tested whether the mean effect size for each species (and vacant cavities), averaged across the eight pairs, was different from zero. For each cluster pair, the effect sizes were calculated as follows:

$$\text{Effect Size} = \Delta_{B_i} - \Delta_{A_i} \quad (3-2)$$

where Δ_{B_i} represents the difference (delta) between the control and removal cluster for pair i (i.e., Control $_i$ – Removal $_i$) during the Before phase, and Δ_{A_i} represents this delta for the After phase. The mean of the Before deltas estimates the average difference between the control and treatment plots in the absence of squirrel removal, or, equivalently, the difference between the control and treatment plots in the event that the removals have no effect (Osenberg et al. 1996). The effect size estimates the magnitude of the effect of the perturbation over and above the inherent and random sources of variation that may cause differences between clusters within a pair. The unit of measurement for effect size is the mean number of cavities per cluster.

If the removals caused a change in the occupancy of a species, the After deltas will be larger in absolute value than the Before deltas (Equation 3-2). In the case of *G. volans*, the After deltas were expected to be positive and larger in absolute value than the Before deltas, resulting in a negative effect size. For *P. borealis*, *M. carolinus*, and Vacant cavities, I predicted that squirrel removal would result in positive mean effect sizes. Because these were *a priori* predictions, I used 1-tailed tests of significance. Also, because of the small sample size ($n = 8$ cluster-pairs), the significance level was set at $\alpha = 0.10$ (Wiens 1989).

Influence of Initial Squirrel Occupancy on Squirrel Effect Size, and the Influence of Squirrel Effect Size on the Other Effect Sizes

Cluster pairs with high squirrel occupancies during the Before phase should have a greater potential for large negative effect sizes for squirrels than cluster-pairs with low initial squirrel occupancy. Also, the effect sizes for *P. borealis*, *M. carolinus*, and *G. volans* were expected to vary inversely with that of squirrels. In order to evaluate these predictions, I calculated the Spearman's rank correlations among these variables, employing 1-tailed tests.

Results

Effects of *G. volans* Removal on Cavity Occupancy

The removal of *G. volans* resulted in a statistically significant reduction in the number of cavities they occupied (mean effect size = -0.390, $t = -1.629$, $n = 8$, $p = 0.074$; Table 3-1). In other words, when accounting for random variation within and between the control and removal clusters, before and after squirrel removal, the removals decreased *G. volans* occupancy by 0.390 cavities/cluster. As predicted, *P. borealis* failed to respond positively to squirrel removal. *Melanerpes carolinus* occupancy, however, increased significantly in response to squirrel removal (Table 3-1). Finally, the removals resulted in a highly statistically significant increase in the number of vacant cavities.

Influence of the Pre-removal Level of Squirrel Occupancy on Squirrel Effect Size

The effect size for squirrels was uncorrelated with their pre-removal occupancy ($r_s = -0.167$, $p = 0.35$, 1-tailed test). Apparently, significant intra- and inter-cluster variation in squirrel occupancy occurred before and after squirrel removal, swamping out any influence of the pre-removal level of squirrel occupancy.

Influence of Squirrel Effect Size on the Effect Sizes for Woodpeckers and Vacant Cavities

The effect sizes for *P. borealis* and *M. carolinus* were negatively associated with the effect sizes for squirrels but both relationships were statistically non-significant ($r_s = -0.190$, $p = 0.325$, and $r_s = -0.357$, $p = 0.193$, respectively). The effect sizes for vacant cavities and *G. volans* were positively correlated, but non-significantly ($r_s = 0.31$, $p > 0.228$).

Discussion

Did the Removals Actually Lower *G. volans* Occupancy?

The purpose of this study was to evaluate the effects of *G. volans* on the occupancy of *P. borealis* cavities by *P. borealis* and *M. carolinus*. Based on previous work (Chapter 2), which proposed the following transitive dominance hierarchy: *G. volans* > *M. carolinus* > *P. borealis*, I predicted that squirrel removal would release *M. carolinus* first, and that the response by *P. borealis* would therefore be weakly positive at best. Of course, any response by the two other species would hinge on the removals actually reducing *G. volans* occupancy. The results clearly indicate that the removals did in fact lower squirrel occupancy. Based on the effect size for squirrels, which incorporated natural variation in the control and removal clusters, before and after the initiation of the removals, squirrel occupancy was 0.39 cavities per cluster lower during the Removal phase compared to the Before phase (Table 3-1A).

Moreover, the removals resulted in an immediate and maintained reduction in squirrel occupancy on the removal plots, relative to the controls (Figure 3-1A). Just prior to the initiation of squirrel removal (spring 2001), mean squirrel occupancy was identical on the control and removal plots (i.e., mean delta of zero; Figure 3-1A). During the first

period of removal, squirrel occupancy on the removal plots dropped by over 0.5 cavities per cluster, a 50% decrease compared to the controls, and this difference (the deltas) was maintained over all four of the Removal-phase time periods (Figure 3-1A).

Response by the Woodpeckers and Vacant Cavities

Consistent with predictions, *P. borealis* failed to respond positively to squirrel removal (Figure 3-1B, Table 3-1). In fact, in comparing the one-year before removal to the Removal phase, *P. borealis* occupancy increased on both the control and removal plots, but more so on the former, resulting in a statistically non-significant, negative effect size (Table 3-1). At least two factors can explain the lack of response by *P. borealis*. First, the positive response by *M. carolinus* may have preempted a response by *P. borealis*. The deltas (Figure 3-1C) indicate that *M. carolinus* occupancy on the removals increased by an average of over 0.45 cavities per cluster during the summer, fall, and winter, when *P. borealis* fledglings and dispersing juveniles and adults are seeking roost cavities. Moreover, because *M. carolinus* and *P. borealis* prefer cavities of similar diameter (Kappes and Harris 1995), *M. carolinus* may have preemptively occupied the most preferred cavities. If true, many of the cavities left vacant by the manipulations may have been the least preferred by both species.

A second factor that may have influenced the lack of a positive response by *P. borealis* is colonization limitation for the small *P. borealis* population studied. That is, relatively few dispersing or prospecting *P. borealis* were around to take advantage of the increased cavity availability where squirrels were removed. *Melanerpes carolinus*, on the other hand, is an abundant species across all woodland habitats in Florida (Cox 1987,

Kale and Maehr 1990) and numerous individuals of this species were on hand to take advantage of the perturbations.

Vacant cavities exhibited the largest effect size, but seasonally they corresponded closely with the response by *M. carolinus*. The strong negative effect size for vacant cavities was driven largely by the dramatic increase in vacant cavities on the Removals during the spring of 2002, the only Removal-phase period in which *M. carolinus* failed to exhibit a response to the removals (Figures 3-1C and 3-1D). Indeed, *M. carolinus* occupancy tended to be relatively low during all three of the spring periods covered by the study (Figure 3-1C). The highest *M. carolinus* occupancies occurred during the colder months, perhaps because of reduced snake activity during this time (Weatherhead 1989, Fitch 1963, Durner and Gates 1993), or because cavities in living trees have warmer and more stable night-time temperatures than cavities in dead trees (Hooge et al. 1999, Wiebe 2001). During the breeding season, *M. carolinus* may have favored sites that were less accessible to snakes (i.e., tall barkless snags), regardless of the availability of *P. borealis* cavities (Kappes 2004). During the first three Removal periods, the mean deltas for Vacant cavities were within 1SE of zero, whereas those for *M. carolinus* were all negative and >1SE from zero, suggesting that many of the cavities made available over these three periods were occupied by *M. carolinus*. *Picoides borealis*'s failure to respond to the large increase in vacant cavities during the spring of 2002 might be attributed to the fact that most annual dispersal and helper recruitment had already occurred by this time.

Some potential unanticipated consequences of squirrel removal. The overall negative, albeit statistically non-significant, response by *P. borealis* may have also

stemmed in part from some unanticipated consequence of squirrel removal. For example, the experiment likely created opportunities for squirrel immigration into the removal clusters. Unlike their predecessors, who were aware of the location and occupancy status of cavities in the cluster, squirrel immigrants might disrupt the social and community structure within the cluster while exploring new cavity resources (Mitchell et al. 1999). If *P. borealis* is more sensitive to such incursions than *M. carolinus*, this might explain the different responses to squirrel removal by the two species. Unfortunately, cavity-associated interactions between squirrels and woodpeckers occur primarily at night, so direct observational evidence is lacking. However, during my efforts to flush the two woodpecker species from their roost or nest cavities (in the process of capturing for banding, or to count eggs or nestlings), *M. carolinus* was notably more difficult to flush than *P. borealis* (JJK, personal observation). If this behavioral difference applies to cavity-associated interactions with *G. volans*, then *P. borealis* may be more readily displaced from cavities by squirrels.

Finally, the poor response by *P. borealis* might have been the result of *M. carolinus* not only seizing cavities made available by squirrel removal, but also increasing its rate of usurpation of *P. borealis* roost cavities. Such an ‘over-response’ by *M. carolinus* might have occurred if transient *M. carolinus* were more likely to remain in removal clusters because of lower encounter rates with squirrels and/or higher cavity availability. Such immigrants might be more likely to displace *P. borealis* for reasons similar to those discussed above for *G. volans*. Subsequent analyses employing Markov models may shed more light on this possibility.

Management Implications

Results of this study suggest that the success of squirrel removal programs, as measured by their benefit to red-cockaded woodpeckers, may vary with community composition. Where other kleptoparasite species are also important, squirrel removal may fail to achieve the desired results, depending on the dominance structure of the community. At my study site, the installation of cavity restrictors (Carter et al. 1989), to prevent *M. carolinus* from occupying the cavities, in conjunction with squirrel removal, might have enabled *P. borealis* to respond positively. Nonetheless, where *G. volans* is the only prominent kleptoparasite, their removal may yield greater benefits for *P. borealis*. In any event, this study points to the need for collecting site-specific heterospecific occupancy information prior to and during the implementation of a removal program. Moreover, management practices should be designed to facilitate periodic evaluation of their effects on target, as well as non-target species. Regular (i.e., at least monthly) cavity inspections, coupled with roost checks, would be required to evaluate the response of *P. borealis* and kleptoparasites to squirrel removal.

Table 3-1. Paired t-tests of the mean occupancy differences (deltas) between the control and treatment clusters (n=8) during the Before phase (July 2000-June 2001) and the *G. volans* Removal phase (July 2001-June 2002).

Species	Δ Before	Δ After	Effect Size ^a	Standard Deviation	t (p-value, 1-tailed)
<i>G. volans</i>	0.114	0.504	-0.390	0.677	-1.629 (0.074)
<i>M. carolinus</i>	-0.049	-0.313	0.264	0.446	1.672 (0.069)
<i>P. borealis</i>	-0.145	0.159	-0.304	0.773	-1.111 (0.152)
Vacant	0.371	-0.278	0.649	0.755	2.430 (0.023)

^aEffect size = Δ Before - Δ After.

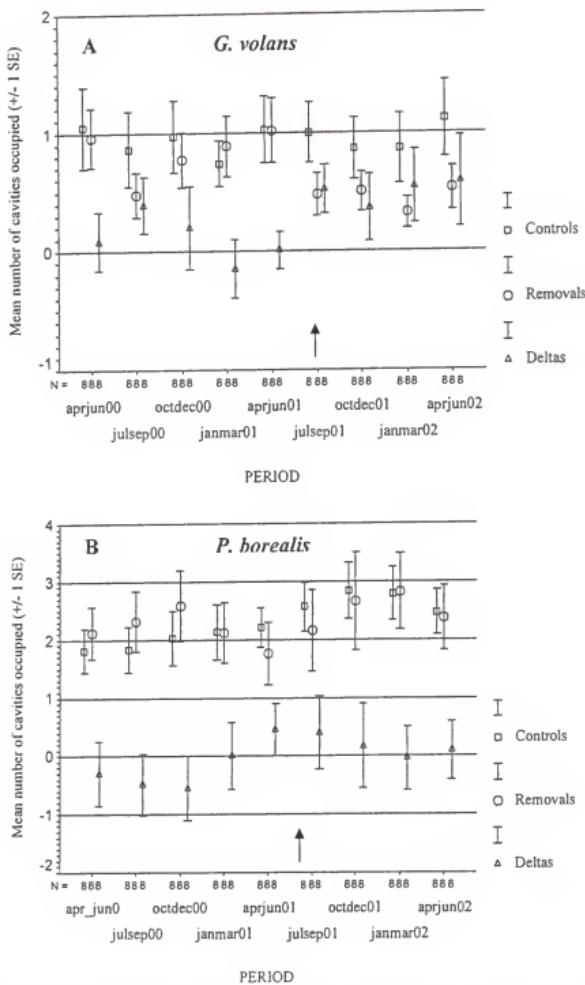


Figure 3-1. Mean number of cavities per cluster occupied (i.e., occupancy; ± 1 SE) by each species in the removal ($n = 8$) and control ($n = 8$) clusters. Arrows designate the initiation of *G. volans* removal (early July 2001). Also shown are the mean deltas (± 1 SE), defined as the mean difference in occupancy (or vacancy) between the control and removal clusters of each cluster pair i (i.e., control $_i$ – removal $_i$). A) *G. volans*. B) *P. borealis*. C) *M. carolinus*. D) Vacant cavities.

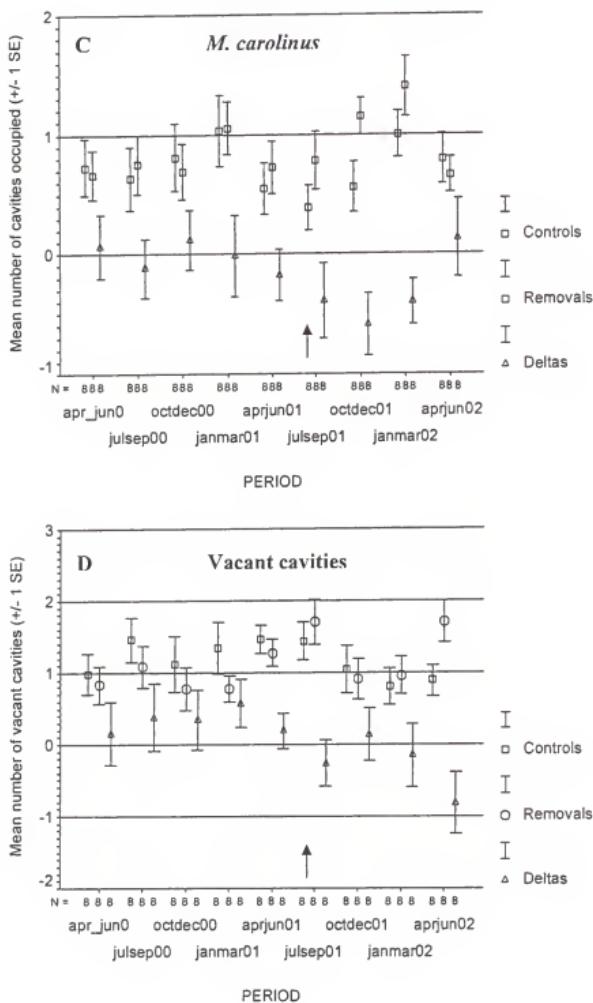


Figure 3-1. Continued

CHAPTER 4
RESIN-BARRIER MAINTENANCE DETERMINES DIFFERENTIAL PREDATION
AMONG OCCUPANTS OF RED-COCKADED WOODPECKER CAVITIES

Introduction

Predation influences ecological community structure through diverse direct and indirect pathways (Paine 1969, Connell 1975, Sih et al. 1985, Holt and Lawton 1994). In avian research, nest predation has received widespread attention recently for its potential role in structuring bird communities (Martin 1988, Wiens 1989, Sieving and Willson 1998, Kullberg and Ekman 2000). A dominant hypothesis is that cup-nesting songbirds experience selective pressure to partition nest-sites to avoid density-dependent functional responses by shared nest-predators (Jeffries and Lawton 1984, Martin 1996, Schmidt and Whelan 1998, Martin and Martin 2001). Li and Martin (1991) suggested that cavity-nesting bird communities may be organized by similar processes. However, essential differences between cavities and cup-nest resources, with respect to their origin and availability, should lead to divergent mechanics of community organization. For example, open cup-nesters normally construct their own nests in substrates that are relatively varied and available (Finch 1982, Wiens 1989, Martin and Li 1992, Newton 1994a, Lindell 1996). In contrast, most cavity nesters depend on a limited supply of pre-existing cavities (Newton 1994b), that are often produced by only one or two local species of excavators (e.g., woodpeckers; Dobkin et al. 1995, Sedgewick 1997, Martin and Eadie 1999, McClelland and McClelland 2000, Martin et al. 2004, Saab et al. 2004). Moreover, potential excavation sites are largely confined to discrete locations within a

forest, i.e., dead or decayed wood of large diameter (Jackson and Jackson 2004). This limited availability and dimensionality of cavity resources constrains niche partitioning in the pursuit of ‘enemy free space’ (Jeffries and Lawton 1984), or in response to interspecific competition. Instead, cavity-nester communities exhibit extensive interspecific overlap in cavity use (Van Balen et al. 1982, Sedgwick and Knopf 1992, Aitken et al. 2002) and interspecific competition and kleptoparasitism over existing cavities (Short 1979, Van Balen et al. 1982, Nilsson 1986, Kerpez and Smith 1990, Finch 1990, Ingold 1994, Newton 1994b, Merila and Wiggins 1995, Kappes 1997). Subordinate individuals or species may be relegated to low-quality sites (Nilsson 1986) or more readily prevented from breeding (e.g., Kerpez and Smith 1990).

On the other hand, because cavity resources are reusable, predation on cavity occupants can render these sites available to other individuals. Moreover, if dominant species are more vulnerable than subordinate ones, shared predators can enhance species coexistence without niche differentiation (Paine 1969, Yodzis 1986, Wootton 2001). This phenomenon, known as ‘predator mediated coexistence’ or ‘keystone predation’, has been reported for various ecological systems (e.g., Paine 1974, Sih et al. 1985, Menge et al. 1994, Henke and Bryant 1999). In this paper, I explore the hypothesis that differential predation by rat snakes (*Elaphe* spp.) enhances coexistence among species occupying red-cockaded woodpecker (*Picoides borealis*) cavities. The potential mechanism of differential predation and coexistence is the ebb and flow of a snake-resistant resin barrier maintained by *P. borealis* but not heterospecific occupants of its cavities.

The Study System

P. borealis is a federally endangered cooperative breeder endemic to the fire-maintained pine forests of southeastern North America. The availability of cavities, which are excavated in living pines, and used for nesting and year-round for roosting, is the primary determinant of territory quality (Ligon 1970, Copeyon et al. 1991, Walters et al. 1992, Davenport et al 2000, USFWS 2003). Cavities require one to several years to excavate but remain suitable for years or even decades. Even after several years of vacancy or occupation by other species, a cavity can be reoccupied by *P. borealis* unless the cavity tree dies or the cavity entrance becomes too enlarged (Baker 1971, Jackson 1978, Doerr et al. 1989, Walters 1990). Sets of cavity trees, termed clusters (Walters 1990), are typically aggregated within a group's territory. The most recently completed cavity usually becomes the breeding male's roost (Conner et al. 1998), which is also used for nesting (Ligon 1970). Breeding females, helpers, and juveniles roost in older cavities, including former nest holes. Cavity shortages cause some group members to roost out in the open, where they may be more vulnerable to predators, inclement weather, and thermoregulatory stress (Kendeigh 1961, Harris and Jerauld 1982, Hooper and Lennartz 1983, Carter et al. 1989). Breeding females and helpers are less likely to remain on cavity-limited territories (Doerr et al. 1989, Carrie et al. 1998, Daniels and Walters 2000). Thus group size, a correlate of group fitness (Davenport et al. 2000, USFWS 2003, Chapter 1), and group stability, can be cavity limited (Carrie et al. 1998, Kappes 2004, Chapter 1).

In southeastern North America, rat snakes (*Elaphe obsoleta* and *E. guttata*) are major predators on cavity nesting birds and southern flying squirrels (*Glaucomys volans*)

(Nolan 1959, Fitch 1963, Conant and Collins 1991, Dennis 1971a, 1971b, Ligon 1970, Jackson 1970, 1974, Hensley and Smith 1986, Neal et al. 1993, Phillips and Gault 1997, Taulman et al. 1998). Rat snakes can readily climb the bark of living pines (Walters 1990, Mullin and Cooper 2002). *Picoides borealis* has apparently adapted to this threat by constructing, and maintaining daily, a snake-resistant resin barrier around its current ('active') nest and roost cavities (Jackson 1974, Jackson 1977a, Rudolph et al. 1990a). However, the resin barrier is ineffective against other species of cavity nesters (Dennis 1971a, Rudolph et al. 1990b, Loeb 1993, Kappes and Harris 1995), which may exacerbate the condition of cavity limitation for *P. borealis* by usurping or preemptively occupying cavities (Kappes 1997, 2004, Chapter 1). Certain heterospecific occupants, such as the great crested-flycatcher (*Myiarchus crinitis*), rarely displace *P. borealis* from cavities but may nonetheless diminish cavity availability for a group. Red-bellied woodpeckers (*Melanerpes carolinus*) and *G. volans*, on the other hand, are dominant over *P. borealis* and commonly usurp active cavities (Ligon 1970, Loeb 1993, Kappes 1997, Chapter 1). However, because heterospecific occupants do not maintain the resin barrier, which dries in a matter of days without maintenance, they should be more vulnerable to snake predation than *P. borealis*. By differentially preying on heterospecific occupants of *P. borealis* cavities, snakes may increase the availability of this limiting resource for *P. borealis*, thereby promoting coexistence. In this paper, I compare daily nest survival rates among *P. borealis* and two avian heterospecific occupants of its cavities in order to evaluate the joint hypotheses that (1) differential predation occurs among species, and (2) if differential predation does occur, it is due to the ebb and flow of the resin barrier. Ideally, I would have examined rates of predation on *G. volans* and all avian

heterospecific occupants. However, predation on squirrels was difficult to distinguish from their frequent movements among multiple den cavities within their territories (Bendel and Gates 1987). Therefore, I studied the nesting success of *M. carolinus* and *M. crinitis*, two avian heterospecific occupants for which sufficient sample sizes could be attained, as models for all heterospecific occupants of *P. borealis* cavities.

Methods

Study Areas

Work was conducted at two sites in northern peninsular Florida: Camp Blanding Training Site (CBTS) in Clay County, and Goethe State Forest (GSF) in Levy County. At CBTS, 60 to 80 *P. borealis* cavities in 13 to 16 clusters were monitored per year from 1995 to 2001. At GSF, 55 to 75 cavities in 13 to 17 clusters were monitored per year between 1996 and 2001. All clusters occurred in mature longleaf pine (*Pinus palustris*) forest. The understory was dominated by saw palmetto (*Serenoa repens*) and wiregrass (*Aristida stricta*). Prescribed fires were conducted at 3-5 year intervals in the study clusters and surrounding forest. I only monitored *P. borealis*-suitable cavities, i.e., those with entrance diameters < 60 mm and which occurred in living trees (Kappes and Harris 1995, Rudolph et al. 1990b). Each cavity was inspected at 10-14 day intervals between April and July using ladders, a drop-light and mirror, or, a video camera mounted on a telescoping pole (TreeTop Peeper, Sandpiper Technologies, Inc., Manteca, California). Once discovered, nests were visited at 1-7 day intervals.

Calculation of Nest Survival Rates

Daily nest survival rates were estimated using the Mayfield method (Mayfield 1961, 1975). Incubation and nestling periods, respectively, for the three study species

were assumed to be 11 and 26 days for *P. borealis* (Labranche and Walters 1994, Winkler et al. 1995), 12 and 26 days for *M. carolinus* (Shackleford et al. 2000) and 14 and 14 days for *M. crinitis* (Taylor and Kershner 1991). Both woodpecker species lay one egg per day, begin incubation before the clutch is complete (Ligon 1970, Jackson 1976, Walters 1990), and have a mean clutch size of about three (JJK, *unpublished data*). Thus, I assumed for both woodpecker species that incubation began upon the deposition of the second egg (Winkler et al. 1995). For *M. crinitis*, I followed Taylor and Kershner (1991) and Miller (2002) and assumed that incubation began upon the deposition of the last egg. Infertile clutches were readily identifiable in the case of the two woodpecker species. Whereas fertile eggs developed from a pink-translucent color when first laid to a non-translucent white before hatching, the eggs of inviable clutches remained pink-translucent over the days of monitoring. A nest was considered depredated if the entire brood of eggs or nestlings disappeared before its estimated date of hatching or fledging. Only two types of predators are known to prey on cavity nesters in this study system, two *Elaphe* spp. (see above) and *G. volans* (Miller 2002; JJK, *Personal observation*). However, in most instances of nest predation, the predator could not be identified directly because it vacated the cavity soon after preying on eggs or young. In such cases, the predator was classified as unknown, but the cavity was examined thoroughly for the following indirect evidence of predator identity. Nests destroyed by *G. volans* usually contain shell fragments or tissue debris (Miller 2002). In contrast, nest predation by snakes, which consume their prey whole, is indicated by virtually undisturbed nest material and the absence of egg or nestling remains (Conry 1988 and references therein). Such indirect evidence of predator identity is considered further in the discussion.

Failure dates were calculated as the midpoint between the date on which the nest was last observed as active and the date on which the failure was discovered (Manolis et al. 2000). Because the observation (exposure) period for a nest was sometimes terminated once an inspection occurred within several days of the estimated fledging date, some failures late in the nestling stage might have gone undetected. I retained such nests of uncertain fate in the sample and terminated their exposure period at the last observed date of activity (Manolis et al. 2000).

If more than one nest was found in a particular cavity within the same breeding season, only the first nest was included in the analysis. A few nests of each species had to be excluded from the Mayfield analysis because they were poorly monitored as a result of access problems. The number of nests found per year, for each species and study area, was usually less than the minimum of 20 required to detect statistical differences among survival rates (Hensler and Nichols 1981). Therefore, I pooled the nest data for each species/study-area combination across years before conducting statistical analyses.

Variances were calculated following Hensler (1985). The null hypothesis of homogenous daily survival rates among the three species was tested using a Chi-square statistic (Sauer and Williams 1989). Separate tests were conducted for the incubation and nestling periods. If the null hypothesis of homogenous daily survival rates among species was rejected, the same test statistic was used to conduct multiple pair-wise tests (Sauer and Williams 1989). Because the lengths of the incubation and nestling phases for *M. crinitis* differed somewhat from those of the two woodpecker species, statistical comparisons among species were restricted to their daily survival rates.

Evaluating Alternatives to the Resin-barrier Hypothesis

In addition to the presence/absence of a resin-barrier, I tested for effects of two other ecological factors that may potentially influence predation rate.

Cavity usurpation status. This alternative is actually complementary to the resin-barrier hypothesis. Nests of kleptoparasites located in recently usurped cavities (i.e., those usurped during that breeding season) might derive some fleeting protection from the diminishing resin barrier. In order to evaluate the influence of cavity usurpation status on nest success, I compared the daily success rates of recently usurped and non-recently usurped cavities. This analysis was restricted to *M. carolinus*, the only avian species that usurped cavities.

Cavity height. Because predation rate can decrease with cavity height (e.g., Nilsson 1984, Rendel and Robertson 1989, Li and Martin 1991), interspecific variation in cavity height could lead to differential predation. Therefore, using pair-wise t-tests, I compared (1) mean nest-cavity height between species and (2) the heights of successful and failed nests within species. I excluded inviable clutches and nests of uncertain fate.

Results

Mayfield Nesting Success

Incubation and nestling periods. Daily survival rates during incubation did not differ among the three species at either GSF or CBTS (Tables 4-1, 4-2). Daily survival rates during the nestling stage, however, exhibited significant differences between *P. borealis* and heterospecific occupants. The relative daily survival rates at both Forests, i.e., *P. borealis* > *M. carolinus* > *M. crinitis* (Table 4-1) were sufficiently different to reject the null hypothesis of equal survival rates (Table 4-2). Pair-wise comparisons

revealed that the daily survival rate of *P. borealis* was significantly higher than both *M. carolinus* and *M. crinitis* at each Forest, but the difference between *M. carolinus* and *M. crinitis* was largely non-significant at both Forests (Table 4-2).

Nest Failure Rates and Causes

For all three bird species, a total of 190 and 163 nests were monitored at GSF and CBTS, respectively (Table 4-3). Failure during the incubation and nestling phases combined occurred for at least 42 (22.1%) of the GSF nests and 43 (26.4%) of the CBTS nests.

Incubation period. Pooling the incubation-stage data across forests and within species, inviable clutches were the most frequent cause of nest failure for *P. borealis* (79% of failures) whereas depredation was the primary cause for both *M. carolinus* and *M. crinitis* (Table 4-3). Inivable clutches occurred for both species of woodpecker but were more frequent for *P. borealis* than *M. carolinus* at both sites (9% vs. 4% of all first nests at GSF and 15% vs. 2% at CBTS). For *M. crinitis*, two (9.5%) of the incubation-stage nests at GSF were depredated, whereas nine (37.5%) of the incubation-stage nests at CBTS were depredated.

Nestling period. At both Forests, depredation was the primary cause of failure during the nestling stage for all three species, causing 90-100% of failures (Table 4-3). Whereas *P. borealis* lost 3-6% of nests that reached the nestling stage, *M. carolinus* and *M. crinitis* lost at least 21-37% of nests that were monitored over that period.

Specific causes of depredation. The specific cause of depredation was documented in only five of 61 cases, all five occurring at CBTS (Table 4-3). *Glaucomys volans* was documented to destroy two *M. carolinus* and two *M. crinitis* nests, primarily

during incubation, and a corn snake (*E. guttata*) consumed a brood of *M. crinitis* nestlings.

Three additional nests that were depredated by known causes, but which were excluded from analysis (see methods), are worth noting. At CBTS, a second *M. carolinus* nest attempt was destroyed during incubation by a *G. volans*. At GSF, two broods of *P. borealis* nestlings were consumed by rat snakes. The first brood (a second nesting attempt) was consumed by an *E. guttata*. The second brood, the only nest that occurred in a dead tree during this study, was preyed upon by an *E. obsoleta*. Both of these *P. borealis* nests occurred in cavity trees that were uniquely accessible to snakes. The first cavity tree had numerous branch stubs that likely helped the snake overcome the resin barrier. The second cavity tree had a defunct resin barrier, having died a year earlier.

Evaluation of Alternative Factors

Cavity usurpation status. I monitored a total of 12 *M. carolinus* nests in recently usurped *P. borealis* cavities (six at each Forest). Unfortunately, this sample was too small to seek statistical inference. Nonetheless, the daily survival rate of these 12 nests was 100%. For comparison, the daily survival rates of non-recently usurped cavities at GSF and CBTS were 0.991 and 0.985, respectively, during incubation, and 0.986 and 0.980, respectively, during the nestling stage.

Cavity height. Cavity height appeared to have little influence on depredation rate. First, mean nest-cavity height did not differ among species ($P > 0.30$; Table 4-4).

Nor did the heights of successful and depredated nests differ within species ($P > 0.40$). For *P. borealis* the mean heights of successful vs. failed nests was similar at both

GSF (8.28 vs. 7.58 m) and CBTS (8.09 vs. 8.24 m). Likewise, successful and failed *M. carolinus* nests were of similar height at both GSF (8.48 vs. 8.02 m) and CBTS (7.44 vs. 8.11 m). Finally, successful and failed *M. crinitis* nests were of similar height at both GSF (7.29 vs. 7.93 m) and CBTS (7.67 vs. 6.50 m).

Discussion

The primary hypotheses of this paper are (1) that heterospecific occupants of *P. borealis* cavities suffer differential predation, and (2) that this differential predation is due to the presence/absence of the resin barrier maintained only by *P. borealis*. The results strongly support both hypotheses. The pattern of relative predation rates at both Forests was as follows: *P. borealis* << *M. carolinus* = *M. crinitis*. These results clearly demonstrate differential predation on the two kleptoparasites I was able to study. Moreover, the foremost explanation for the observed pattern is the presence/absence of the resin barrier, which is highly effective against rat snakes but not other predators. The barrier deteriorates quickly when the cavity is not occupied by *P. borealis*, thereby rendering heterospecific occupants more vulnerable to snakes. Even so, *M. carolinus* may have derived a modicum of protection from the evanescent resin barriers of recently usurped cavities. Unfortunately, low sample sizes precluded any reliable inferences from being drawn. Nonetheless, about 12% of *M. carolinus* nests occurred in recently usurped cavities, perhaps accounting for its marginally lower depredation rate compared to *M. crinitis*, which almost invariably used cavities with defunct resin barriers.

Direct and Indirect Effects of Snakes on *P. borealis*

These results suggest that snakes have at least two effects on *P. borealis* (Figure 4-1). The first is predation on eggs, nestlings, and adults (P_{PE}), a direct effect which is

weakened considerably by the resin barrier. The second is a positive indirect effect composed of a sequence ($P_{KE} P_{PK}$) of direct negative effects (an interaction chain; Wootton 1994). That is, by preying on heterospecific occupants of *P. borealis* cavities, snakes lessen the effect of kleptoparasites on cavity limitation. If the magnitude of the facilitative indirect effect exceeds that of the direct effect of predation (i.e., $P_{KE} P_{PK} > P_{PE}$), the net effect of snakes on *P. borealis* will be positive (Figure 4-1).

Of course, the net effect of snakes on *P. borealis* will vary across habitats (Menge et al. 1994) with (1) the extent of the predation differential ($P_{KE} - P_{PE}$), (2) *Elaphe* abundance and behavior, and (3) the strength of the effect of kleptoparasites on *P. borealis* (P_{PK}). All else equal, the predation differential should increase with resin-barrier quality (as defined by host-tree pitch production, the extent of the resin-well system, and ultimately by the barrier's effectiveness against snakes) because better resin barriers decrease the magnitude of P_{PE} disproportionately relative to P_{KE} . Factors that influence the quality of the resin-barrier include pine species, stand structure, duration of cavity use by *P. borealis*, and the incidence of helpers (reviewed by Kappes 2004).

Alternatives to the Resin-barrier Hypothesis

I conducted tests of two factors that could influence nest predation in my study system, besides the resin-barrier hypothesis. Here I discuss those and two others that I was not able to test directly.

Cavity usurpation status. The limited data I had to evaluate this alternative strongly suggests that heterospecifics breeding in a recently usurped *P. borealis* cavity, with a recently maintained resin barrier, receive fleeting protection from nest predation. However, more data are needed to fully test this hypothesis.

Cavity height. I found no evidence that cavity height influenced the pattern of differential predation. Nest cavity height did not differ among species, nor did the mean heights of successful and depredated nests differ within species. These results suggest that active resin barriers protected even the lowest *P. borealis* nests. Conversely, cavities without active resin barriers were accessible to snakes regardless of height (Walters 1990, Mullin and Cooper 2002). Indeed, a corn snake preyed on a *M. crinitis* nest in the highest cavity monitored at CBTS (14 m).

Physical nest defense. Another possible explanation for the observed pattern of differential predation is that *P. borealis* is superior at physically defending its nests from predators, but the available evidence suggests otherwise. Although the data needed to evaluate the dominance relationship between *P. borealis* and *M. crinitis* is lacking, *M. carolinus* is clearly dominant over *P. borealis* in cavity-associated interactions, commonly displacing it from roost and nest cavities (Ligon 1970, Kappes 1997, Chapter 2). Thus, assuming transitivity in the physical relationships among species in this community (including predators), it seems unlikely that *P. borealis* is better than *M. carolinus*, at least, at fending off nest predators.

Snakes vs. squirrels as predators. *Glaucomys volans* was observed in depredated cavities more often than snakes (Table 4-3), suggesting that squirrels may have been important nest predators. Moreover, squirrels were observed preying on other kleptoparasites, but not on *P. borealis*, suggesting that they may have contributed to the pattern of differential predation. If so, the observed pattern might constitute diffuse differential predation, rather than keystone predation (Menge et al. 1994). However, the weight of the evidence supports the conclusion that snakes were the primary nest-

predators, and the principal cause of differential predation. In most instances, shell fragments, tissue debris, or other prey remains were absent, implicating snakes as the cause (Conry 1988 and references therein). Furthermore, the fact that differential predation occurred consistently during the nestling period, but not during incubation, points to snakes because they prey on nests primarily after hatching (Jackson 1970, 1977b; Hensley and Smith 1986; Eichholz and Koenig 1992; Neal et al. 1993, Richardson and Stockie 1995), whereas *G. volans* depredates cavity nests primarily during incubation (Miller 2002, this study). Also, the proportion of cavities occupied by squirrels at CBTS was over three times as high as at GSF (18% vs. 6%; Chapter 2); yet, the pattern of differential predation was the same at the two Forests, again implicating snakes as the common dominant cause. Finally, if squirrels were major nest predators, one would have expected them to destroy more *P. borealis* nests, given their dominance over this woodpecker, and their immunity to the resin barrier.

I propose that snakes were seldom seen in the monitored cavities because they rarely lingered after depredating a nest. The snakes I did observe typically departed by the next day. In contrast, telemetry work has shown that rat snakes may den in tree cavities for 1-2 weeks during ecdysis or digestion (Durner and Gates 1993). Perhaps *P. borealis*-suitable cavities are too small for such use, especially by larger snakes. Indeed, anecdotal information indicates that snake occupation of enlarged *P. borealis* cavities is greater (Loeb 1993, JJK, pers. observ.). If true, snake visitation to *P. borealis*-suitable cavities may be largely restricted to foraging activities. As such, given the cavity-nesting habits of *G. volans*, it is not surprising that snakes were observed less frequently than squirrels in depredated cavities.

In any event, even if squirrels had contributed to the observed pattern of differential predation, this would not detract from the asserted role of snakes. *Glaucomys volans* itself is often the most important member of the kleptoparasite guild (Chapter 2). Thus, snakes act as keystone predators for *P. borealis* by preying differentially on squirrels, as well as other kleptoparasites. Moreover, differential predation by squirrels would be less likely to actually increase cavity availability for *P. borealis* because squirrels may depredate nests largely in the pursuit of cavity resources. The suggested scenario of snakes as 'hit and run' predators (see above paragraph) indicates that snakes are far more likely to 'renew' cavities for *P. borealis*.

Implications for Conservation

Many biologists consider rat snake predation on *P. borealis* to be an important management issue. In fact, three management tools, including the use of snake nets (Neal et al. 1993, Samano et al. 1998), bands of aluminum flashing (Montague et al. 1995), and a bark-shaving technique (Saenz et al. 1999), have been developed to protect *P. borealis* from snakes. The results of this paper, however, suggest that anti-snake practices could lead to unexpected consequences. In particular, snake exclusion could truncate the facilitative indirect effect of snakes on *P. borealis*. Although these techniques may be useful when applied to active cavity trees with compromised resin barriers, especially in small *P. borealis* populations, they should be applied with caution pending further research on this issue. Any cavities receiving such treatment should be monitored for occupancy. If the cavity becomes vacated by *P. borealis*, snake exclusion should be discontinued.

Also, snake exclusion may occur inadvertently as a result of the way managers mark *P. borealis* cavity trees. A standard practice is to scrape and paint white bands on cavity trees to make them more conspicuous during potentially damaging activities (e.g., prescribed fire, military training, logging). Such bands are often wide enough to simulate the Saenz et al. (1999) method of snake exclusion. Since these painted bands are placed on every known cavity tree in the population, widespread protection of heterospecific occupants may occur, with negative consequences for *P. borealis*. Thus, research is needed to determine the optimal band width; i.e., one that maximizes visibility without excluding snakes. Meanwhile, the bands should be kept as narrow as possible (perhaps 15 cm), or they should be reduced to four spots of white around the bole, leaving bark in between.

Experimental exclusion of snakes from *P. borealis* cavity-tree clusters will be required to fully establish a causal link between snakes and cavity availability for *P. borealis*. Such experiments would also help to further elucidate the relative roles of snakes and squirrels as predators in this system, as well as their interactions with each other as predator and prey. Finally, research is needed to determine how much the strength of the direct and indirect effects of snakes vary, across the range of *P. borealis*, with snake abundance, intensity of kleptoparasitism, and host-tree characteristics.

Table 4-1. Mayfield estimates of the daily survival rates of red-cockaded woodpeckers (*Picoides borealis*), red-bellied woodpecker (*Melanerpes carolinus*), and great crested-flycatcher (*Myiarchus crinitis*) at GSF and CBTS.

Nest Period	Site	Species	Daily survival		Mayfield nesting success ^a		
			N	rate	SD	SD	
Incubation	GSF	<i>P. borealis</i>	101	0.981	0.005	0.814	0.046
		<i>M. carolinus</i>	46	0.992	0.004	0.911	0.049
		<i>M. crinitis</i>	21	0.990	0.007	0.872	0.085
Incubation	CBTS	<i>P. borealis</i>	68	0.978	0.006	0.787	0.057
		<i>M. carolinus</i>	51	0.986	0.006	0.841	0.059
		<i>M. crinitis</i>	24	0.957	0.014	0.537	0.111
Nestling	GSF	<i>P. borealis</i>	102	0.997	0.001	0.924	0.030
		<i>M. carolinus</i>	48	0.986	0.004	0.700	0.072
		<i>M. crinitis</i>	19	0.957	0.016	0.544	0.125
Nestling	CBTS	<i>P. borealis</i>	62	0.998	0.001	0.960	0.028
		<i>M. carolinus</i>	49	0.982	0.005	0.629	0.078
		<i>M. crinitis</i>	15	0.967	0.016	0.627	0.146

^a Mayfield estimate of success for the nest period (i.e., incubation or nestling), calculated as s^j , where s = the daily survival rate and j = the number of days in the period.

Table 4-2. Statistical contrasts of the Mayfield nesting success of the three species.

Nest stage	Site	Contrast	χ^2	P
Incubation	GSF	Overall ^a	2.694	0.260
		<i>P. borealis</i> vs. <i>M. carolinus</i>		
		<i>P. borealis</i> vs. <i>M. crinitis</i>		
		<i>M. carolinus</i> vs. <i>M. crinitis</i>		
Incubation	CBTS	Overall	3.765	0.152
		<i>P. borealis</i> vs. <i>M. carolinus</i>		
		<i>P. borealis</i> vs. <i>M. crinitis</i>		
		<i>M. carolinus</i> vs. <i>M. crinitis</i>		
Nestling	GSF	Overall	12.630	0.002
		<i>P. borealis</i> vs. <i>M. carolinus</i>	6.670	0.010
		<i>P. borealis</i> vs. <i>M. crinitis</i>	6.264	0.012
		<i>M. carolinus</i> vs. <i>M. crinitis</i>	3.182	0.074
Nestling	CBTS	Overall	14.750	0.001
		<i>P. borealis</i> vs. <i>M. carolinus</i>	11.220	0.001
		<i>P. borealis</i> vs. <i>M. crinitis</i>	3.733	0.053
		<i>M. carolinus</i> vs. <i>M. crinitis</i>	0.808	0.369

^aTests the null hypothesis of equal survival rates among the three species.

Table 4-3. Number and cause (if known) of nesting failures for three species. Numbers given are minimum estimates, except for the 'unknown predator' category.

Species	N	Number failed ^a	Inviably clutch ^b	Total number depredated ^b	Con-specific intruder ^c	Flying squirrel	Rat snake	Unknown predator ^d
Goethe State Forest - Incubation								
<i>P. borealis</i>	101	13 (12.9%)	9 (69.2%)	3 (23.1%)	1 (7.7%)			3 (23.1%)
<i>M. carolinus</i>	46	3 (6.5%)	2 (66.6%)	1 (33.3%)				1 (33.3%)
<i>M. crinitis</i>	21	2 (9.5%)		2 (100%)				2 (100%)
Camp Blanding Training Site - Incubation								
<i>P. borealis</i>	68	11 (16.2%)	10 (90.9%)	1 (9.1%)				1 (9.1%)
<i>M. carolinus</i>	51	4 (7.8%)	1 (25%)	3 (75%)		1 (25%)		2 (50%)
<i>M. crinitis</i>	24	9 (37.5%)		9 (100%)		2 (22.2%)		7 (77.8%)
Goethe State Forest – Nestling period								
<i>P. borealis</i>	102	6 (5.9%)		6 (100%)				6 (100%)
<i>M. carolinus^e</i>	48	11 (22.9%)		10 (90.9%)				10 (90.9%)
<i>M. crinitis</i>	19	7 (36.8%)		7 (100%)				7 (100%)
Camp Blanding Training Site – Nestling period								
<i>P. borealis</i>	62	2 (3.2%)		2 (100%)				2 (100%)
<i>M. carolinus^f</i>	49	13 (26.5%)		12 (92.3%)		1 (7.7%)		11 (84.6%)
<i>M. crinitis</i>	15	4 (26.7%)		4 (100%)		1 (25%)		3 (75%)

^a Percent of all nests (N). ^b Percent of failures. ^c Not included in depredated category.

^d Shell fragments and tissue debris were absent in nearly all instances, implicating snakes (Conry 1988). ^e One nest destroyed by flooding. ^f One nest lost to starvation.

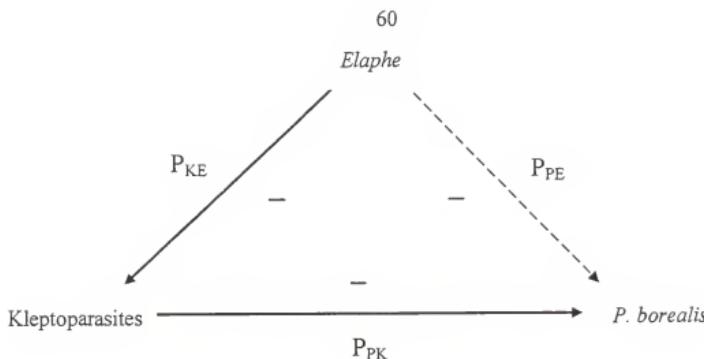


Figure 4-1. Community interaction web modeling ecological interactions among rat snakes (*Elaphe* spp.), *P. borealis*, and kleptoparasites of *P. borealis* cavities. P_{PE} represents the direct, negative (−) effect of *Elaphe* predation on *P. borealis* group-fitness, P_{KE} is the direct negative effect of snake predation on cavity occupancy by kleptoparasites, and P_{PK} is the cavity-associated, direct negative effect of kleptoparasites on group fitness. Arrow widths are proportional to relative interaction strengths.

CHAPTER 5
MULTISPECIES OCCUPANCY DYNAMICS OF
RED-COCKADED WOODPECKER CAVITIES: A MARKOV MODEL ANALYSIS

Introduction

A primary aim of ecology is to predict the effects of competing management schemes or other perturbations on ecological systems; but logistical factors often limit the amount of empirical information available to make such predictions (Wootton 1994, Marschall and Roche 1999). Mathematical models provide an alternative approach to forecasting ecosystem dynamics (Kareiva 1989), and a tool for steering ongoing empirical work (Werner 1999). The challenge is to select the appropriate modeling framework and which parameters to include. Ecological communities associated with spatial resources are particularly amenable to Markov chain models (Wootton 2001a, b), which have been applied to plant community dynamics (e.g., Waggoner and Stephens 1970, Horn 1975), termite succession (Usher 1979), beaver pond dynamics (Pastor et al. 1993), and marine benthic communities (Tanner et al. 1994, 1996; Wootton 2001a,b). In this chapter, I use simple Markov chain models to examine the multispecies occupancy-dynamics of red-cockaded woodpecker (*Picoides borealis*) cavities.

Picoides borealis cavities are the focus of a complex web of ecological interactions that determine their patterns of occupancy. For example, heterospecific occupants (cavity kleptoparasites; Kappes 1997), especially red-bellied woodpeckers (*Melanerpes carolinus*) and southern flying squirrels (*Glaucomys volans*), exacerbate cavity limitation for *P. borealis* (Chapter 2). Also, rat snakes (*Elaphe* spp.) prey on the

occupants of these cavities, including *P. borealis* nestlings and roosting adults. Because *P. borealis* is an endangered species, the above interactions have often prompted managers to remove or exclude kleptoparasites (especially *G. volans*; Richardson and Stockie 1995, Montague et al. 1995, Gaines et al. 1995, USFWS 2003), and rat snakes (Neal et al. 1993, Withgott et al. 1995, Saenz et al. 1999). However, the net effects of these practices are poorly studied. When kleptoparasite and predator management is evaluated in the context of the whole community, including direct and indirect effects among species, the potential for unanticipated consequences becomes apparent. For example, because of the following dominance hierarchy among the primary occupants of *P. borealis* cavities: *G. volans* > *M. carolinus* > *P. borealis*, squirrel removal may first benefit *M. carolinus*, which in turn preempts an occupancy response by *P. borealis* (Chapters 2 and 3). Also, rat snake exclusion may lead to unanticipated consequences because these predators may bestow beneficial indirect effects (increased cavity availability) on *P. borealis* by preying differentially on cavity kleptoparasites (Kappes 2004, Chapter 4). Although further empirical research is needed, Markov models provide a powerful framework with which to synthesize existing data, predict the net effects of species interactions and management on *P. borealis*, and to explore the dynamics of community structure.

The specific objectives of this Markov model analysis are to (1) Describe the breeding season occupancy dynamics of *P. borealis* cavities at short (10-14 day) census intervals, which reflect the influence of species interactions and short-term colonization on community composition. (2) Describe the occupancy dynamics of cavities at long census intervals (one-year), including an additional analysis that compares the pattern of

cavity occupancy by *P. borealis* breeding males to other *P. borealis* (breeding females and helpers) as it relates to other species and vacant cavities. (3) Systematically evaluate the relative importance of component species and their interactions to the long-term composition and stability of the community; this analysis includes a model test of the effects of kleptoparasite removal on *P. borealis* occupancy. (4) Simulate the effects of snake exclusion on the long-term composition of the community in order to evaluate the hypothesis that snake exclusion has a negative net-effect on *P. borealis*. (5) Describe the successional trajectory of the community as predicted by the annual model beginning with 100% vacant cavities. (6) Evaluate the effects of actual *G. volans* removal on transition structure using data from the field experiment presented in Chapter 3.

Markov Models of Ecological Communities

Multispecies Markov models are composed of square transition matrices (\mathbf{P}) and column vectors (\mathbf{X}_t). The elements of \mathbf{P} are probabilities (p_{ij}) that a point occupied by ecological state j at census interval t , will be occupied by ecological state i at $t + 1$. In this paper, ecological states include different species and vacant cavities. The matrix is read such that each transition moves *from* the ecological state at the head of the column *to* the ecological state at the head of the row, from one census interval to the next. Transitions from a species to empty space may indicate predation, whereas the reverse signifies colonization. Transitions between species may point to interference interactions or the net effect of more complex processes. Of course, caution is warranted in inferring any particular process as the cause of a particular transition. For instance, the confidence with which any transition can be inferred as a specific process depends on the census interval (Wootton 2001b, Usher 1979).

The elements (x_i) of the column vector X_t represent the proportion of points (woodpecker cavities in this case) that are in each ecological state at time t . Given X_t , one can predict the communities composition at $t + 1$ (X_{t+1}) by multiplying the column vector X_t by the transition matrix P . That is:

$$X_{t+1} = P X_t \quad (5-1)$$

By iterating this process, one can predict the community's composition further into the future. Assuming that the elements of the matrix P remain constant, the community eventually converges on the equilibrium community composition, X^* , at which the proportion of points in each ecological state reaches a steady state. This equilibrial community composition is analogous to the stable age distribution of Leslie matrices (Leslie 1945, Caswell 2000), and is given by the dominant eigenvector (of the matrix) standardized so that its elements sum to one.

As in the analysis of population matrix models, Markov model analysis focuses on the response of the eigenvalues and eigenvectors of P to changes in the elements of the transition matrix (Tanner et al. 1994, Caswell 2000, Wootton 2001a). In population models, the dominant eigenvalue (λ_1) corresponds to the population growth rate. In Markov models, however, the first eigenvalue always equals one. Therefore, eigenvalue analysis focuses on the ratio of the first and second eigenvalues (λ_1/λ_2), known as the return time or damping ratio. This ratio indicates how rapidly the community returns to its equilibrium community composition following a disturbance (Tanner et al. 1994), and is considered an index of community resilience (Wootton 2001a, citing Caswell 1989, DeAngelis 1989) or dynamic stability (Horn 1975). The larger the ratio, the faster the system will return to its equilibrium, and thus the greater its resilience. Markov model

analysis also examines the response of the equilibrium community composition (again, given by the dominant eigenvector) to alterations of the transition matrix. Assumptions of the simple Markov chain models used in this paper include (1) that the transition matrix is derived from a first order Markov chain (i.e., the probability that a point will move to ecological state i at time t depends only on its state at $t-1$), and (2) that the transition probabilities are constant.

Methods

Data Collection and Model Parameterization

Transition probabilities were derived from repeated censuses of *P. borealis* cavities at two Forests in northern peninsular Florida: Camp Blanding Training Site (CBTS) in Clay County, and Goethe State Forest (GSF) in Levy County. Field data was incorporated into three sets of transition matrices: (1) a breeding season matrix for each forest, (2) an annual matrix for each Forest, and (3) a set of before-after control-removal matrices based on a *G. volans* removal experiment conducted at CBTS (Chapter 3). Data for the first two sets of matrices were collected as follows. Cavities were censused every 10-14 days (see below: *Cavity Monitoring*) from April to July for a total of 7-9 censuses/cavity/year. At CBTS, 60 to 80 *P. borealis* cavities in 13 to 16 clusters were censused between 1995 and 2001. At GSF, 55 to 75 cavities in 13 to 17 clusters were censused between 1996 and 2001. Breeding season matrices were derived by pooling data within and between years. The transitions in the breeding season models represent the probability of a cavity moving from one ecological state to another over the 10-14 day census interval. Annual matrices were derived by pooling data across years. The transitions in the annual matrix represent the probability of a cavity moving from one

dominant ecological state to another between years, where each year's dominant ecological state is the one that occurred most frequently during the 7-9 censuses conducted between April and July. When ties occurred, the tied state observed first during that year was considered the dominant.

The third set of matrices was based on a *G. volans* removal experiment conducted at CBTS (Chapter 3). The experiment was conducted year-round from July 2000 to June 2002 employing a paired, before-after, control-removal design in 16 cavity clusters. I monitored cavity occupancy in all 16 clusters throughout the two-year period. No squirrels were removed during a pre-removal phase (July 2000-June 2001). In July 2001, I established eight cluster pairs according to their mean proportion of cavities that were occupied by *G. volans* during April-May of 2001, and randomly designated the members of each cluster pair as a control or removal based on a coin toss. During the second year of the study, the removal phase (July 2001-June 2002), I removed any squirrels encountered in the removal clusters during cavity monitoring. Four transition matrices were constructed for analysis: (1) a pre-removal matrix for the eight control clusters, (2) a pre-removal matrix for the eight removal clusters, (3) a removal-phase matrix for control clusters, and (4) a removal-phase matrix for removal clusters.

Cavity monitoring

The same basic methods of cavity monitoring were used to generate all matrices. I only monitored *P. borealis*-suitable cavities, i.e., those with entrance diameters <60 mm and which occurred in living trees (Kappes and Harris 1995, Rudolph et al. 1990b). New cavities were added to the census schedule as they appeared. Cavity trees that died during the study were excluded from subsequent censuses but I retained data collected

while the tree was alive. Each cavity was inspected at 10-14 day intervals using ladders, a drop-light and mirror, or, a video camera mounted on a telescoping pole (TreeTop Peeper, Sandpiper Technologies, Inc., Manteca, California). I also noted the presence or absence of resin-well maintenance by *P. borealis*. If the cavity was empty, but exhibited abundant evidence of fresh resin-well work, I assumed the cavity was occupied by *P. borealis* at that census interval. If the cavity contained *G. volans* (a nocturnal species), avian eggs or nestlings, or any other taxon, I recorded the appropriate species as the occupant. If the cavity was empty and exhibited no evidence of fresh resin-well maintenance, it was re-visited that night and checked for roosting birds using an infra-red option on the video camera. Night-time inspections would usually reveal either an empty cavity or a roosting *M. carolinus*. If the cavity was empty during the day-time inspection and exhibited marginal evidence of resin-well maintenance by *P. borealis*, or if the resin-well status had changed since the previous census, the cavity was re-visited for a pre-sunset roost check in which an observer watched the cavity to determine if any birds entered it to roost. Roost checks enabled me to determine a cavity's occupancy status without disturbing any bird that may have recently occupied the cavity.

The following five ecological states, which accounted for >99% of inspections, were included in the Markov models: *P. borealis*, *M. carolinus*, *G. volans*, vacant cavities, and Passerines [great-crested flycatcher (*Myiarchus crinitus*), tufted titmouse (*Parus bicolor*), and Eastern bluebirds (*Sialia sialis*)]. Passerines were collapsed into one category because of small sample sizes and their similarity in cavity-nesting ecology. Additionally, in the analysis of the annual models, *P. borealis* was divided into two

demographic categories: breeding males and other *P. borealis*, the latter category consisting primarily of breeding females and helpers.

Model Analyses

Unless otherwise stated, model analysis followed closely the methods of Wootton (2001), and focuses primarily on comparing (1) the equilibrium community composition and (2) the return time (λ_1/λ_2) of altered matrices with their unmanipulated form. In general, more weight is given to the equilibrium community composition. Because all columns in a Markov model must sum to one, all non-target transitions in a column that was affected by a transition manipulation (see below) were adjusted in proportion to their magnitude so that the column summed to one. Once an appropriately manipulated matrix was developed, I compared the similarity of its predicted stable-stage distribution to that of the unmanipulated model using:

$$\text{Similarity} = 1 - \left[\sum_{i=1}^s \sqrt{(p_{u,i} - p_{m,i})^2} \right] / 2 \quad (5-2)$$

where $p_{u,i}$ is the predicted proportion of cavities occupied by ecological state i in the unmanipulated community, $p_{m,i}$ is the predicted proportion of cavities occupied by ecological state i in the manipulated community, s is the number of ecological states included in the model, and \sqrt is the square root (Wootton 2001a).

The effect of a matrix manipulation on return time was evaluated by analyzing the factor change in return time (time factor) between the unmanipulated model and its altered version. The time factor was calculated as: $\ln(1/\lambda_{2u})/\ln(1/\lambda_{2m})$, where λ_{2u} and λ_{2m} are the subdominant eigenvalues of the manipulated and unmanipulated models, respectively (Wootton 2001a, following Caswell 1989). A time factor of around one

indicates no manipulation effect on recovery time. A time factor of >1 indicates a slowing of return time and <1 indicates an acceleration. For example, a time factor of 1.09 indicates that the manipulation causes a 9% slower return time and a time factor of 0.85 indicates a 15% faster return time (Wootton 2001a).

Species removals.

In order to simulate the complete removal of a species, all transitions involving the target state were set to zero and the remaining ecological states in the column were increased in proportion to their magnitude so that all columns summed to one. Because the similarity index for each species is a function of (1) the target species' abundance in the unmanipulated matrix, and (2) the influence of the transitions involving the target species (i.e., its interaction strength; Tanner et al. 1994), I also derived a standardized similarity index in which the similarity calculated using Equation 5-2 was divided by the relative number of cavities occupied by the target ecological state in the unmanipulated model at equilibrium. The relative number of cavities occupied was calculated by multiplying the proportion of cavities occupied at equilibrium by 100.

Sensitivity and elasticity analyses

Following Wootton (2001a) I conducted sensitivity analysis by systematically reducing each matrix element by an amount equal to one-half of the smallest non-zero transition probability present in either the CBTS or GSF version of the model, and proportionally allocating this amount to the other elements in the column so that the column summed to one. I conducted an elasticity analysis by reducing each element by an amount equal to 50% of the target transition and allocating this amount to the

remaining elements in the column in proportion to their magnitude so that the column summed to one.

Effects of kleptoparasites on cavity occupancy by *P. borealis*. Of particular interest in the species removal, sensitivity and elasticity analyses is the effect of kleptoparasites on the remaining species in the model, especially *P. borealis*. Thus, in order to use the models to explore the effects of *P. borealis* displacement by kleptoparasites, I simply extracted the relevant results from the species removal, sensitivity, and elasticity analyses, rather than conducting a separate, and perhaps redundant analysis of these interactions.

Simulating snake exclusion

Prior work suggested that by preying differentially on kleptoparasites of *P. borealis* cavities, rat snakes (*Elaphe spp.*) may indirectly benefit *P. borealis* by increasing cavity availability (Chapter 4). Furthermore, I concluded that snakes rarely remain in *P. borealis*-suitable cavities after preying on their contents. Thus the effects of snake predation are a component of transitions to vacant cavities (Tanner et al. 1994). Moreover, predation-induced transitions to vacant cavities occur at the expense of self-replacement by the victim. As such, I explored the potential indirect effect of snake exclusion on *P. borealis* by simultaneously increasing the self-replacement rates of all three kleptoparasite species, taking the increase for each from its respective transition to vacant status. To derive a biologically relevant level of manipulation, I assumed that the observed pattern of transition from *M. carolinus* to vacancy was representative of general predation rates on kleptoparasites. Indeed, whereas *G. volans* move about multiple cavities within a cluster and passerines use the cavities only for a brief (28 day) nesting

period, *M. carolinus* tends to occupy cavities continuously for roosting and nesting. Thus some transitions from squirrels or passerines to vacant status may result from movements or successful fledging, rather than snake predation, whereas transitions from *M. carolinus* to vacancy are more likely to indicate predation. I explored the effects of different levels of snake exclusion by increasing kleptoparasite self-replacement from zero (the unmanipulated models) to 0.06 (nearly complete snake exclusion) by increments of 0.02. (Note: the increase in self-replacement is constrained by the rate of transition from *M. carolinus* to vacancy, which is 0.075 and 0.091 at CBTS and GSF, respectively; Table 5-1). Because the resin barrier maintained by *P. borealis* renders it relatively immune to snake predation (Rudolph et al. 1990, Chapter 4), I assumed that snake exclusion would have a negligible effect on *P. borealis* self-replacement rates. I used the breeding season models because snakes are most active during this period and because the breeding season census intervals are most relevant to predation effects on kleptoparasite self-replacement rates.

Results

Unmanipulated Models

Breeding season models. The largest transitions at both sites were the self-replacement rates for the five ecological states (in bold, Table 5-1). The self-replacement rates of the four taxa were strikingly similar between Forests but that for vacant cavities was 22% higher at GSF. Other relatively large transitions at both sites were reciprocal transitions between *G. volans* and vacant cavities (although the rate of *G. volans* colonization was nearly three times greater at CBTS) and transitions from passerines to vacant cavities. The primary difference between the two forests was that the rates of

transition to *G. volans* from the other ecological states were 3-7 times higher at CBTS than at GSF; this finding is consistent with the dramatically higher rates of cavity occupancy by *G. volans* at CBTS (Chapter 2).

Eigenvector analysis predicted a community dominated by *P. borealis* at both Forests (Table 5-3). However, *G. volans* occupancy at CBTS was expected to be over 2.4 times greater at CBTS. Correspondingly, *P. borealis* occupancy was over 30% greater at GSF. The remaining community components were similar at the two sites. The first and second eigenvalues indicated a slightly faster return time at CBTS (1.074) than at GSF (1.070).

Annual models. The magnitudes of the annual transition rates were more evenly distributed than those of the breeding season transitions (Table 5-2). The largest terms at both Forests were again self-replacement by *P. borealis*, *M. carolinus*, *G. volans*, and vacant cavities, but the magnitudes of these transitions were considerably lower than in the breeding season models. Reciprocal transitions between *G. volans* and vacant cavities were again relatively large except for *G. volans* colonization at GSF which was again less than one-third the rate at CBTS. The two Forests differed primarily in the rates of transition to *G. volans* from other ecological states, most notably *M. carolinus*, which were substantially higher at CBTS. Also, GSF exhibited a five-fold greater colonization rate by *M. carolinus*.

Eigenvector analysis again predicted *P. borealis* to be dominant at GSF (Table 5-3). At CBTS, however, the equilibrial occupancy of *P. borealis* barely exceeded that of *G. volans*, which in turn occupied a 3.5 fold greater proportion of cavities at CBTS than at GSF. *Melanerpes carolinus* accounted for a 46% greater proportion of the community

at GSF than at CBTS. The damping ratios indicated a faster return time at CBTS (1.666) than at GSF (1.613).

By dividing the *P. borealis* category in the annual matrix into (1) breeding males and (2) breeding females and helpers, several interesting trends were revealed (Figure 5-1). The trends common to both forests are as follows. Perhaps most striking is that no transitions from any other ecological state to breeding males were observed, indicating that breeding males, which typically occupy the nesting cavity, shun cavities that have been occupied previously by other species. Also, breeding males exhibited a 46-66% lower rate of interspecific displacement, and a 30-36% greater self-replacement rate, than other *P. borealis*. The largest inter-state transitions were between the breeding female/helper category and the non-*P. borealis* ecological states (Figure 5-1). The rate of transition from breeding males to other species exceeded the rate of transition from breeding males to *P. borealis* females/helpers. The most notable differences between forests were the moderately higher self-replacement rates by both *P. borealis* demographic categories at GSF. Also, rates of female/helper displacement by *G. volans* was far higher at CBTS, and female/helper displacement by *M. carolinus* was higher at GSF.

Model Manipulations

Sensitivity and elasticity analyses for species composition

The sensitivities of the breeding-season model predictions to small reductions (0.00042) in each transition exhibited a distribution skewed towards negligible effects at both sites (Table 5-4). The highest sensitivities (lowest similarities) at both sites were almost exclusively for transitions from *P. borealis*, followed by transitions to *P. borealis*.

The lowest sensitivities at both sites were for transitions moving from passerines to non-*P. borealis* ecological states.

The sensitivities of the annual models to small reductions (0.00407) in each transition exhibited less skewed distributions than the breeding season models at both sites (Table 5-5). At CBTS and GSF, transitions from *P. borealis* again accounted for most of the largest sensitivities but at CBTS transitions from *G. volans* to *P. borealis* also exhibited a high sensitivity. The lowest sensitivities at both sites were again those moving from passerines.

The elasticities for both the breeding season and annual models from both sites exhibited more skewed distributions than the sensitivity analyses (Tables 5-6 and 5-7). All four model/site combinations predicted that the 50% reduction in self-replacement by *P. borealis* would have by far the greatest effect on species composition, this element invariably being a distant outlier (Tables 5-6 and 5-7). For the breeding season model at CBTS, the next largest community responses were to the altered self-replacement rates of *M. carolinus*, vacant cavities, and *G. volans*, and the transition from *G. volans* to vacant cavities. At GSF, self-replacement of vacant cavities and *M. carolinus*, and *P. borealis* colonization, had the next largest effects (Table 5-6).

The elasticity analysis of the annual model for CBTS indicated that *G. volans* self-replacement, transitions from *G. volans* to *P. borealis*, *G. volans* colonization, and transitions from *P. borealis* to *M. carolinus*, had relatively large effects on community composition (Table 5-7). At GSF, transitions from *P. borealis* to *M. carolinus*, *M. carolinus* self-replacement, and colonization by *P. borealis* and *M. carolinus* also had relatively large effects on model predictions.

Of particular interest to managers are the relative effects of *P. borealis* displacement by their two major cavity kleptoparasites, *M. carolinus* and *G. volans* (Figure 5-2). In general, the sensitivity analyses of the four model/site combinations indicated that the small reduction in the rate of displacement by *M. carolinus* and *G. volans* would have similar effects on *P. borealis*'s equilibrium occupancy. The far larger reduction (50%) imposed by the elasticity analyses yielded more variation in model responses. The breeding season models for CBTS predicted that *P. borealis* would respond similarly to a dramatic reduction in displacement by *M. carolinus* or squirrels. At GSF, however, *P. borealis*'s predicted response to reduced rates of displacement by *M. carolinus* was 10 times greater than its response to reduced rates of displacement by *G. volans*. Elasticity analysis of the annual models forecasted a greater response to *M. carolinus* at both sites, although the difference was far more pronounced at GSF.

Sensitivity and elasticity analyses for return times

At both sites, as with the effects on community composition, transitions moving from *P. borealis* to the other ecological states had the largest effects on recovery time, followed by transitions moving to *P. borealis*, especially its self-replacement rate (Table 5-8). Recovery time accelerated in response to the small reduction in *P. borealis* self-replacement but slowed in response to reductions in all other transitions involving *P. borealis*. The two sites differed in that the GSF breeding season model also predicted more rapid returns to equilibrium as a result of the small reductions in self-replacement by *M. carolinus*, *G. volans*, and vacant cavities. The sensitivity analyses of the annual models for both sites also indicated that the small reductions in transitions moving away

from *P. borealis* would increase return time and that the reduction in *P. borealis* self-replacement would cause a relatively large acceleration of return time (Table 5-9).

Not surprisingly, the effects of 50% reductions in individual transitions had more noticeable and widespread effects on model predictions. Both the breeding season and annual models from both sites predicted that perturbing *P. borealis* self-replacement would have the largest effects, decreasing return times in the breeding season and annual models by over 60% and 50%, respectively (Tables 5-10 and 5-11). The breeding season models also predicted notably faster (>5%) return times as a result of reducing the self-replacement rates of *M. carolinus* at GSF, *G. volans* at CBTS, and vacant cavities at both sites (Table 5-10). The annual models predicted notable effects for reducing the self-replacement rates of *G. volans* at CBTS (Table 5-11). All four model/site combinations also predicted that the 50% reductions in transitions moving away from *P. borealis*, especially those moving to *M. carolinus* and vacant cavities at both sites, and those moving to *G. volans* at CBTS, would slow return times. Both the breeding season and annual models also predicted notable effects from perturbing the colonization rates of *P. borealis* at both sites, *M. carolinus* at GSF, and *G. volans* at CBTS; return times slowed with decreased *P. borealis* colonization and accelerated with reduced *M. carolinus* and *G. volans* colonization.

Species removals

For all four model/site combinations, the removal of *P. borealis* had the largest effects on predicted community composition, although these effects were greater at GSF than at CBTS (Table 5-12), Figures 5-3 to 5-6). The breeding season models for both sites predicted that *P. borealis* removal would cause vacant cavities to become the

dominant ecological state, whereas the annual models predicted that *G. volans* would dominate cavity occupancy at CBTS and *M. carolinus* would co-dominate with vacant cavities at GSF (Figures 5-3 and 5-4). The only other substantial removal effect (similarity <0.7; Table 5-12) was that predicted by the CBTS annual model for *G. volans*, whose removal in general was predicted to cause large changes in species composition at CBTS and minimal changes at GSF. In contrast, *M. carolinus* removal was predicted to have a relatively large effect on community composition by the GSF annual model, largely because of a dramatic positive response by *P. borealis* (Figure 5-6), and moderate effects (similarity 0.80-0.85) by the three other model/site combinations. All four model/site combinations predicted that passerine removal would have relatively negligible effects on species composition. In comparing the effects of removing the two primary kleptoparasites, the four model/site combinations predicted that *P. borealis* would respond more to *G. volans* removal at CBTS (especially in the breeding season model) and that it would respond dramatically more to *M. carolinus* at GSF (Figures 5-5 and 5-6).

Consistent with the predicted effects of species removal on community composition, all model/site combinations predicted that *P. borealis* removal would have the most consistently large effect on return time, a 39-58% faster return to equilibrium, and that passerine removal would have minimal effects (Table 5-4). The removal of *M. carolinus* and vacant cavities consistently slowed the rate of return to equilibrium, *M. carolinus* by 7-33% and vacant cavities by 6-247%. In contrast, *G. volans* exhibited no consistent or interpretable trend across sites and models, unlike its effects on species composition.

Snake exclusion

P. borealis's predicted equilibrial occupancy decreased across the range of snake exclusion levels at both sites. However, *M. carolinus*, and to a lesser extent *G. volans* and passerines, exhibited a greater positive response at GSF. As a result, the decrease in *P. borealis* occupancy was more marked at GSF than at CBTS (9.44% vs. 3.48% at the highest level of snake exclusion; Figure 5-7). *Melanerpes carolinus* exhibited a slightly exponential increase across the range of snake-exclusion levels at both sites. Compared to the unmanipulated models, predicted *M. carolinus* occupancy at the highest level of snake exclusion was 51% higher at CBTS and 59% higher at GSF. Vacant cavities decreased steadily across the range of exclusion, exhibiting an over 20% decrease at the highest level at both sites.

Successional patterns

Beginning with 100% vacant cavities, the annual models predicted that both communities would reach their equilibrial composition within 8-9 years (Table 5-3, Figure 5-8). At CBTS, over 70% of the cavities were occupied by year one, most by *G. volans*, which remained the dominant species through year three. The two woodpecker species, which exhibited lower annual colonization rates but higher self replacement rates than *G. volans* at CBTS (Table 5-2), increased gradually to their equilibrial occupancies, with *P. borealis* surpassing *G. volans* by year six.

At GSF, over 60% of cavities became occupied by year one. *Picoides borealis*'s pattern of occupancy over time was similar to that at CBTS. The GSF model differed from CBTS primarily with respect to the patterns of occupancy exhibited by *M. carolinus* and *G. volans*. First, *M. carolinus*'s colonization rate at GSF was dramatically higher

than that for any other species/ site combination except *G. volans* at CBTS. Thus, *M. carolinus* became the dominant species after one year, but then declined gradually to its equilibrium occupancy, being superseded by *P. borealis* at year two. *Glaucomys volans*, a relatively minor species at GSF, peaked at one year and then declined gradually to its steady state occupancy of 8%. At both sites, passerines exhibited a small peak at one or two years before declining to its low equilibrial occupancy.

Based on the highest probabilities of transition from each ecological state to other states, individual cavities exhibited the following annual pattern of occupational succession at the two sites (Figure 5-1, Table 5-2). *Picoides borealis* breeding males primarily occupied new cavities, usually for 2-3 years at CBTS and for 3-4 years at GSF. At CBTS, cavities were then equally likely to become occupied by *M. carolinus* or *P. borealis* females/helpers, which in turn are eventually replaced by *G. volans*. Older cavities at CBTS fall into an alternating pattern of vacancy and high rates of occupancy by *G. volans*. At GSF, *P. borealis* breeding males are most likely to be replaced directly by *P. borealis* females/helpers, which are then most likely to be replaced by *M. carolinus*. Older cavities at GSF are most likely to alternate between occupancy by *M. carolinus* and vacancy.

G. volans Removal Experiment

G. volans removal caused a large reduction in squirrel self-replacement, with transitions from squirrels moving instead to vacant cavities and especially to *M. carolinus*; the latter transition increased more than 10-fold (Table 5-13F). *Melanerpes carolinus* also increased its colonization rate, whereas this rate actually decreased slightly for *P. borealis*. Also, although the matrix-manipulation results reported above indicated

little impact of passerines on the community, squirrel removal nonetheless increased rates of passerine self-replacement, apparently by reducing the rate of transition to squirrels (Table 5-13F).

The matrix models of the control and removal clusters during the pre-removal and removal phases predicted that the equilibrium occupancy of *G. volans*, and to a lesser extent, *M. carolinus*, would respond most to squirrel removal. The long-term occupancies in the control and removal clusters, respectively, decreased by 10.5% and 60% for *G. volans*, increased by 4% and 15% for *M. carolinus*, and increased by 21.7% and 27.1% for *P. borealis* (Figure 5-15).

Discussion

The Markov models effectively captured many realistic aspects of the study communities that were reported in previous chapters. In particular, the models described known between-site differences with respect to the importance of squirrels, the dominant species in terms of interference interactions associated with *P. borealis* cavities (Chapters 2 and 3). Moreover, the models captured the dynamics associated with between-site differences in squirrel occupancy. Interspecific transitions moving to squirrels, reciprocal transitions between squirrels and vacant cavities, and the equilibrium occupancy by squirrels, were all notably higher at CBTS than at GSF. Correspondingly, the 22% higher rate of persistence by vacant cavities and the five-fold greater *M. carolinus* colonization rate at GSF, were attributable to the lesser role of squirrels at that site. As a result, model manipulations generally pointed to a greater importance of *P. borealis* and *M. carolinus* at GSF. Model predictions indicated that passerines had minimal influence on community dynamics at both sites, presumably because they were relatively

ephemeral occupants (using the cavities only for nesting) and they replaced other species at extremely low rates.

Although *G. volans* is dominant in interference interactions, the analyses also described well the numerical importance of *P. borealis* at both sites (especially GSF). Analyses confirmed that this species' dominance derives from its high rate of self-replacement; this was especially evident in the shorter-term breeding season models (but also in the annual models). Sensitivity analyses of the breeding season models and, to a lesser extent the annual models, indicated that any source of *P. borealis* turnover, breaking the chain of cavity occupancy, caused relatively large changes in equilibrium species composition (Tables 5-4 and 5-5). In contrast, the larger transition reductions imposed by the elasticity analyses indicated that *P. borealis* self-replacement had the largest effects (by far) on species composition using both the breeding season and annual models from both sites (Tables 5-6 and 5-7). The difference between the sensitivity and elasticity analyses was due to the fact that the small changes in *P. borealis* self-replacement imposed by the sensitivity analyses had insignificant effects on equilibrial composition because this element remained the largest even after its reduction. The larger changes imposed by the elasticity analysis, however, reduced *P. borealis*'s equilibrial occupancy to only 4%, with corresponding increases in the remaining ecological states. This caused a substantial deviation in overall species composition from the unmanipulated model.

The sensitivity, elasticity, and species removal analyses indicated that *P. borealis* also had the greatest effect on return time, which indicates how fast a community would return to equilibrium following a disturbance (i.e., a displacement from its steady state

composition), and which has been proposed as an index of community resilience (Wootton 2001a, citing Caswell 1989, DeAngelis 1989). All model/site combinations predicted that removing *P. borealis* or reducing its self-replacement rate would dramatically increase the community's rate of recovery. Similarly, all model/site combinations predicted that reducing the rates of transition from *P. borealis* to any other ecological state would slow recovery. Thus the presence of *P. borealis* negatively affected community resilience, as defined above. The removal of *M. carolinus*, in contrast, invariably had the greatest destabilizing effect among the four taxa, indicating that the presence of this kleptoparasite enhanced community resilience (Table 5-12).

The above findings do not impugn the status of *P. borealis* as a keystone cavity excavator in this ecosystem (Kappes 2004). Instead, they illustrate the fact that the simple models I employed focused on the occupancy dynamics of existing cavities. A more complex model that incorporated cavity production by *P. borealis* would likely yield different results with respect to *P. borealis*'s effects on community stability. Nonetheless, *P. borealis*'s negative effect on community resilience in the simple models I used is actually not surprising. "Copious" rates of self-replacement, like those exhibited by *P. borealis* (Tables 5-1 and 5-2), actually slow a community's rate of recovery (Horn 1975). Indeed, in the successional analysis starting with 100% vacant cavities, *P. borealis* was the last species to reach its steady state (Figure 5-8).

In comparison to two previous studies employing Markov models, my study indicated, as did Wootton's (2001a) study of a marine intertidal community, that the transitions most important to community structure were self-replacement by the dominant species and transitions moving from it. In contrast, Tanner et al.'s (1994) study of coral

reefs concluded that no one species was particularly important and that transitions to free space had the largest effects on community dynamics. Differences among ecosystems in such patterns are likely explained by life history variation among the component species, especially with respect to their patterns of persistence and colonization (Tanner et al. 1994).

Snake Exclusion

The negative effects of snake exclusion on *P. borealis* at both sites, as simulated, stemmed primarily from the large positive response by *M. carolinus*. *Melanerpes carolinus* exhibits relatively low rates of transition to other ecological states, enabling it to capitalize the most on increased rates of self-replacement (decreased predation). *Glaucomys volans*, in contrast, exhibited little or no response to snake exclusion at either site because its high rate of transition to vacancy counterbalanced the effects of increased self-replacement. Nonetheless, the difference in the magnitude of response by *P. borealis* at the two sites stemmed largely from differences in the importance of *G. volans*. At CBTS, higher rates of all transitions moving to *G. volans*, and from *G. volans* to vacancy, resulted in an occupancy sink that inhibited the response by it and the other kleptoparasites in comparison to GSF. As a result, kleptoparasites exhibited an overall larger response at GSF, and this in turn caused a greater decrease in *P. borealis*.

The role of snakes in the *P. borealis* cavity system may explain apparent discrepancies between previous work, which indicated a clear dominance hierarchy among the three primary cavity occupants: *G. volans* > *M. carolinus* > *P. borealis* (Chapters 2, 3), and the observed rates of transition among the three species (Table 5-1). The breeding season model from CBTS, where all three species were well represented,

only bears out the dominance of *G. volans* over *M. carolinus*. Indeed, *G. volans* displaced *M. carolinus* at a rate four times greater than the reverse transition (Table 5-1). Breeding season transitions between *P. borealis* and the two primary kleptoparasites, in contrast, appeared to reflect a high of degree reciprocity. I suggest however, that this apparent reciprocity is not the result of *P. borealis* “holding its own” in interference interactions. Instead, I propose that many transitions from kleptoparasites to *P. borealis* are not direct displacements, but the result of cavities becoming available following snake predation on the kleptoparasite. Indeed, previous workers have also noted how predators not included in the Markov models may influence the rates of transition between species (Tanner et al. 1994, Wootton 2001).

Although the breeding season models were used to simulate the effects of decreased snake predation, the annual models may also reflect the influence of snakes on patterns of cavity occupation. In particular, repeated snake visitation to particular cavities may prevent kleptoparasites from monopolizing these cavities, thereby increasing the probability that the site will be available for colonization by *P. borealis* females and helpers, which subsequently establish a protective resin barrier and are able to occupy the cavity with relative impunity.

Annual Models-Succession

In the successional analysis beginning with 100% vacant cavities, some species (e.g., *G. volans* and passerines at both sites, *M. carolinus* at GSF) quickly overshot their equilibrium before being “damped out” (Figure 5-8; Tanner et al. 1994). Such patterns can be explained by within-site temporal changes (succession), and between-site variation, in community composition. Species that peaked early and then declined did so

because early transitions *to* these species, particularly from vacant cavities, exceeded rates of transition *from* them. As cavity occupancy by other species increased and the availability of empty cavities declined, however, the early colonists were damped out by transitions to empty cavities and/or other species until they reached their equilibrial balance of losses and gains. Although *M. carolinus* self-replacement rates were nearly identical and relatively high at the two sites, its successional trajectory exhibited the greatest between-site difference because of variation in squirrel importance. At CBTS, where squirrels were abundant and rapid colonizers, *M. carolinus* exhibited a relatively low colonization rate, a high rate of transition to squirrels, and a gradual but continuous ascent to equilibrium (Table 5-2, Figure 5-8). At GSF, where squirrels were relatively unimportant, *M. carolinus* colonization was more than five-times greater, but its rate of transition to vacant cavities was also considerably higher. As a result, *M. carolinus* occupancy at GSF peaked at year one and then descended slowly to its equilibrium. *Glaucomys volans* at CBTS exhibited the highest colonization rate and succeeded other species at high rates, but it also had the highest rate of transition to vacant cavities. As a result, squirrels reached a high peak after one year and then declined slowly while (decreasingly) inhibiting the ascent of the two woodpecker species and damping passerines. At GSF, passerines peaked at year two and were then damped down by transitions moving to other ecological states, especially *P. borealis*. *Picoides borealis*, in contrast slowly achieved the highest equilibrial occupancy at both sites with low colonization rates but high self-replacement rates.

The successional trajectory predicted by the annual model is most representative of cavities added to existing clusters, or artificial clusters established by managers in

habitat frequented by prospecting *P. borealis* (assuming ubiquity of the remaining species as well). Nonetheless, the pattern of initial squirrel dominance predicted by the annual model is reminiscent of the high rates of squirrel occupancy reported to occur by managers in recruitment clusters with low potential for *P. borealis* colonization (R. Costa, pers. comm.). Moreover, the pattern of cavity occupancy by *P. borealis* suggests that once cavities have remained vacant or occupied by heterospecifics for most of a breeding season, they may be shunned by breeding males thereafter. These findings support the recommendation that managers avoid establishing more recruitment clusters than they can reasonably expect to be occupied by *P. borealis* in the short term (USFWS 2003).

The version of the annual model with *P. borealis* demographic categories (Figure 5-1) indicated that breeding females and helpers frequently used cavities that had been either vacant (16-19%) or occupied by kleptoparasites (25%) during the previous breeding season (Figure 5-1). This demonstrates my previous assertion that even older cavities, including those used extensively by other species, remain critical resources for a group, playing a crucial role in the attraction and retention of females and helpers. As discussed above, rat snakes may facilitate such recolonization. However, such cavities were shunned by breeding males, suggesting that many groups that lose their nest cavity to kleptoparasites may forgo reproduction unless a new cavity is or becomes available. In about 10% of cases, breeding males used cavities that had been used by other group members during the previous breeding season, when the chambers of such cavities were sufficiently completed for roosting purposes, but still too narrow to accommodate a breeding male and nestlings.

G. volans Removal Experiment

The Markov model analysis of the field removal experiment supported the primary conclusion of Chapter 3, i.e., that *M. carolinus* responded more positively to squirrel removal than did *P. borealis*. Moreover, the model added mechanistic detail to this conclusion. Accounting for random temporal variation, and inherent differences between the control and removal clusters, the rate of transition from *G. volans* to *M. carolinus* increased by more than 10-fold between the pre-removal and removal phases, indicating that *M. carolinus* often took swift (i.e., before the next census) advantage of the cavities made available (Table 5-13). Additionally, transitions from vacancy to *M. carolinus* increased with squirrel removal. These responses by *M. carolinus* possibly precluded any positive response by *P. borealis*.

The Markov model simulation of complete squirrel removal at CBTS also seemed to do a good job of predicting *M. carolinus*'s response as a non-target kleptoparasite (Figures 5-3 to 5-6). Both the breeding season and annual models for CBTS predicted that *M. carolinus* would respond to squirrel removal (proportionally) at least as much as *P. borealis*, thereby limiting the benefits accrued by the latter. Also, although no field removal of *G. volans* was conducted at GSF, the models predicted that squirrel deletion at GSF would have minimal effects on *P. borealis* and other species in the community. This finding points to the need for understanding the structure of the community in which *P. borealis* is embedded at any particular locale before expending resources on *G. volans* removal.

Although the actual (experimental) and simulated removal of squirrels both predicted a large positive response by *M. carolinus*, the approaches predicted different

responses by *P. borealis*. *P. borealis* failed to respond positively to actual squirrel removal, perhaps because it was preempted from doing so by *M. carolinus* (Chapter 3, Table 5-13). In contrast, the model simulation predicted a positive response by both species (Figure 5-5). I examined this discrepancy by conducting a transience analysis of the predicted response by the two woodpecker species. Unlike the previous simulated removals, which evaluated removal effects on equilibrial (long term) occupancy, transience analysis characterizes both the short-term and long-term dynamics of the community (Hill et al. 2002). In the transience analysis, both species exhibited rapid increases immediately following squirrel removal before leveling off to their asymptotic occupancies (Figure 5-10). These results indicate that the model simulation of squirrel removal failed to reproduce the preemptive short-term response by *M. carolinus* that was evident in the experiment. However, this discrepancy could also be an artifact of the time scale used to derive the model (Wootton 2001b). Indeed, the fact that field removal of squirrels increased the rate of transition from *G. volans* to *M. carolinus* by over 10-fold indicates that the census interval was too long to capture the obvious intermediate transition (from *G. volans* to vacancy) that occurred immediately following squirrel removal. In other words, a shorter census interval might have yielded larger increases in transitions from *G. volans* to vacancy, and from vacancy to *M. carolinus* (colonization). If *M. carolinus* colonization occurs over a shorter time interval than *P. borealis*, the model may have overestimated *P. borealis*'s capacity to respond (to squirrel removal) relative to *M. carolinus*. If true, a simulation using a model derived from shorter census intervals might have yielded a more rapid and preemptory response by *M. carolinus*.

Another simulation with obvious management implications was the deletion of *M. carolinus* from the models, which is tantamount to adding cavity restrictors to all *P. borealis* cavities in a population, effectively setting to zero all transitions involving *M. carolinus* but having no direct effects on the other species included in the models (Carter et al. 1999, Walters 1991, Loeb 1993, Raulston 1996). Unlike the simulated and field removal of *G. volans*, simulated *M. carolinus* exclusion (cavity restriction) had large positive effects on *P. borealis*, and minimal effects on the remaining species (except *M. carolinus* of course) for all model/site combinations (Figures 5-3 to 5-6). This finding is consistent with the proposed dominance hierarchy among the three primary cavity occupants (see above). Whereas the potential benefits accrued by *P. borealis* as a result of squirrel removal are partially offset by a positive response by *M. carolinus*, which ranks second after *G. volans* in the hierarchy, the models predict that when *M. carolinus* is removed *P. borealis* exhibits a relatively exclusive positive response.

Table 5-1. Breeding season (April-July) transition matrices pooled across years for two northern Florida study sites. Transitions are for 10-14 day census intervals.

To:	From:				
	<i>P. borealis</i>	<i>M. carolinus</i>	<i>G. volans</i>	Vacant	Passerines
Camp Blanding Training Site					
<i>P. borealis</i>	0.958	0.021	0.015	0.032	0.000
<i>M. carolinus</i>	0.014	0.863	0.009	0.048	0.031
<i>G. volans</i>	0.015	0.038	0.609	0.258	0.078
Vacant	0.012	0.075	0.358	0.640	0.313
Passerines	0.001	0.002	0.009	0.022	0.578
Goethe State Forest					
<i>P. borealis</i>	0.964	0.014	0.006	0.054	0.013
<i>M. carolinus</i>	0.013	0.870	0.025	0.045	0.013
<i>G. volans</i>	0.002	0.014	0.679	0.092	0.026
Vacant	0.021	0.091	0.284	0.775	0.355
Passerines	0.001	0.011	0.006	0.034	0.592

Table 5-2. Annual transition matrices for the dominant ecological state that occurred over 7-9 censuses conducted each year between April and July at two northern Florida Forests.

To:	From:				
	<i>P. borealis</i>	<i>M. carolinus</i>	<i>G. volans</i>	Vacant	Passerines
Camp Blanding Training Site					
<i>P. borealis</i>	0.741	0.105	0.140	0.162	0.000
<i>M. carolinus</i>	0.114	0.474	0.128	0.054	0.000
<i>G. volans</i>	0.076	0.281	0.488	0.432	0.500
Vacant	0.057	0.140	0.209	0.297	0.333
Passerines	0.013	0.000	0.035	0.054	0.167
Goethe State Forest					
<i>P. borealis</i>	0.789	0.136	0.120	0.189	0.333
<i>M. carolinus</i>	0.130	0.477	0.080	0.270	0.167
<i>G. volans</i>	0.008	0.068	0.400	0.135	0.167
Vacant	0.073	0.250	0.360	0.378	0.167
Passerines	0.000	0.068	0.040	0.027	0.167

Table 5-3. Predicted stable stage distributions for different unmanipulated Markov models.

Ecological state	Model							
	Breeding season	Breeding Season	Annual CBTS	Annual GSF	Control Before	Control After	Removal Before	Removal After
	CBTS	GSF	CBTS	GSF				
<i>P. borealis</i>	0.357	0.472	0.335	0.437	0.396	0.482	0.376	0.478
<i>M. carolinus</i>	0.148	0.155	0.164	0.239	0.148	0.154	0.169	0.194
<i>G. volans</i>	0.208	0.086	0.307	0.088	0.181	0.162	0.196	0.079
Vacant	0.267	0.259	0.165	0.206	0.272	0.196	0.247	0.234
Passerines	0.020	0.028	0.029	0.030	0.003	0.006	0.012	0.015

Table 5-4. Sensitivity analysis of transition effects on species composition for the breeding season models. Numbers shown are the similarities (see text for calculations) between the manipulated model and the unmanipulated model for the manipulation of the corresponding transition.

To:	From:				
	<i>P. borealis</i>	<i>M. carolinus</i>	<i>G. volans</i>	Vacant	Passerines
Camp Blanding Training Site					
<i>P. borealis</i>	0.99850	0.99900	0.99865	0.99825	NA
<i>M. carolinus</i>	0.99775	0.99970	0.99950	0.99935	0.99995
<i>G. volans</i>	0.99780	0.99960	0.99960	0.99970	1.00000
Vacant	0.99785	0.99960	0.99985	0.99950	1.00000
Passerines	0.99765	0.99960	0.99975	0.99970	0.99995
Goethe State Forest					
<i>P. borealis</i>	0.99835	0.99895	0.99945	0.99850	1.00000
<i>M. carolinus</i>	0.99695	0.99950	0.99975	0.99940	1.00000
<i>G. volans</i>	0.99710	0.99965	0.99975	0.99965	1.00000
Vacant	0.99745	0.99965	0.99990	0.99945	1.00000
Passerines	0.99725	0.99965	0.99985	0.99970	0.99995

Table 5-5. Sensitivity analysis of transition effects on species composition for the annual models. Numbers shown are the similarities (see text for calculations) between the manipulated model and the unmanipulated model for the manipulation of the corresponding transition.

To:	<i>P. borealis</i>	<i>M. carolinus</i>	<i>G. volans</i>	Vacant	Passerines
From:					
		Camp Blanding Training Site			
<i>P. borealis</i>	0.99740	0.99840	0.99700	0.99835	NA
<i>M. carolinus</i>	0.99710	0.99900	0.99805	0.99895	NA
<i>G. volans</i>	0.99710	0.99905	0.99835	0.99915	0.99980
Vacant	0.99705	0.99915	0.99850	0.99925	0.99995
Passerines	0.99630	NA	0.99835	0.99920	0.99980
Goethe State Forest					
<i>P. borealis</i>	0.99695	0.99760	0.99910	0.99795	0.99970
<i>M. carolinus</i>	0.99590	0.99870	0.99940	0.99880	0.99985
<i>G. volans</i>	0.99570	0.99850	0.99945	0.99870	0.99975
Vacant	0.99630	0.99885	0.99955	0.99900	0.99985
Passerines	NA	0.99880	0.99950	0.99905	0.99985

Table 5-6. Elasticity analysis of transition effects on species composition for the breeding season models. Numbers shown are the similarities (see text for calculations) between the manipulated model and the unmanipulated model for the manipulation of the corresponding transition.

To:	<i>P. borealis</i>	<i>M. carolinus</i>	<i>G. volans</i>	Vacant	Passerines
From:					
		Camp Blanding Training Site			
<i>P. borealis</i>	0.68615	0.97375	0.97420	0.92600	NA
<i>M. carolinus</i>	0.95820	0.89225	0.99460	0.95850	0.99805
<i>G. volans</i>	0.95580	0.98115	0.92065	0.92195	0.99810
Vacant	0.96645	0.96220	0.91935	0.89440	0.99015
Passerines	0.99585	0.99905	0.99780	0.99320	0.99195
Goethe State Forest					
<i>P. borealis</i>	0.58665	0.98225	0.99605	0.87455	0.99730
<i>M. carolinus</i>	0.94795	0.88515	0.99310	0.96050	0.99875
<i>G. volans</i>	0.99420	0.99390	0.95795	0.96415	0.99895
Vacant	0.92250	0.94215	0.94815	0.85475	0.98285
Passerines	0.99725	0.99475	0.99935	0.98945	0.98835

Table 5-7. Elasticity analysis of transition effects on species composition for the annual models. Numbers shown are the similarities (see text for calculations) between the manipulated model and the unmanipulated model for the manipulation of the corresponding transition.

To:	From:				
	<i>P. borealis</i>	<i>M. carolinus</i>	<i>G. volans</i>	Vacant	Passerines
Camp Blanding Training Site					
<i>P. borealis</i>	0.83695	0.97695	0.93945	0.96395	NA
<i>M. carolinus</i>	0.95130	0.95520	0.96730	0.99280	NA
<i>G. volans</i>	0.96995	0.96285	0.92365	0.94735	0.99030
Vacant	0.97775	0.98415	0.96010	0.97525	0.99400
Passerines	0.99420	NA	0.99320	0.99470	0.99740
Goethe State Forest					
<i>P. borealis</i>	0.77630	0.95405	0.98500	0.94230	0.98605
<i>M. carolinus</i>	0.91660	0.93840	0.99460	0.95530	0.99600
<i>G. volans</i>	0.99570	0.98710	0.97950	0.97820	0.99525
Vacant	0.96230	0.95910	0.97715	0.95990	0.99650
Passerines	NA	0.98945	0.99765	0.99685	0.99735

Table 5-8. Sensitivity analysis of transition effects on return time for the breeding season models. Numbers shown are the factor changes in return time of the breeding season Markov models resulting from a 0.00042 reduction in the corresponding transition.

To:	From:				
	<i>P. borealis</i>	<i>M. carolinus</i>	<i>G. volans</i>	Vacant	Passerines
Camp Blanding Training Site					
<i>P. borealis</i>	0.99684^a	1.00158	1.00317	1.00317	NA
<i>M. carolinus</i>	1.00636	0.99999	0.99999	0.99999	0.99999
<i>G. volans</i>	1.00636	0.99999	0.99999	0.99999	0.99999
Vacant	1.00636	0.99999	0.99999	0.99999	0.99999
Passerines	1.00796	0.99999	0.99999	0.99999	0.99999
Goethe State Forest					
<i>P. borealis</i>	0.99545	1.00148	1.00148	1.00300	0.99997
<i>M. carolinus</i>	1.00604	0.99846	0.99997	0.99846	0.99997
<i>G. volans</i>	1.00604	0.99997	0.99846	0.99846	0.99997
Vacant	1.00452	0.99997	0.99997	0.99846	0.99997
Passerines	1.00604	0.99997	0.99997	0.99846	0.99997

^a Factor change in return time was calculated as $\ln(1/\lambda_{2u})/\ln(1/\lambda_{2m})$, where λ_{2u} and λ_{2m} are the subdominant eigenvalues of the unmanipulated and manipulated Markov models, respectively.

Table 5-9. Sensitivity analysis of transition effects on return time for the annual Markov models. Numbers shown are the factor changes in return time resulting from a 0.00407 reduction in the corresponding transition.

To:	From:				
	<i>P. borealis</i>	<i>M. carolinus</i>	<i>G. volans</i>	Vacant	Passerines
	Camp Blanding Training Site				
<i>P. borealis</i>	0.98964^a	0.99903	1.00888	1.00426	NA
<i>M. carolinus</i>	1.01219	1.00033	0.99740	0.99870	NA
<i>G. volans</i>	1.01020	1.00033	0.99740	0.99870	1.00000
Vacant	1.00921	1.00000	0.99870	0.99935	1.00000
Passerines	1.01352	NA	0.99642	0.99805	0.99968
	Goethe State Forest				
<i>P. borealis</i>	0.99093	1.00200	1.00437	1.00539	1.00098
<i>M. carolinus</i>	1.01222	0.99896	0.99930	0.99795	0.99963
<i>G. volans</i>	1.01222	0.99930	0.99795	0.99795	0.99930
Vacant	1.01085	0.99963	0.99896	0.99829	0.99963
Passerines	NA	1.00031	1.00098	1.00098	0.99997

^a Factor change in return time was calculated as $\ln(1/\lambda_{2u})/\ln(1/\lambda_{2m})$, where λ_{2u} and λ_{2m} are the subdominant eigenvalues of the unmanipulated and manipulated Markov models, respectively.

Table 5-10. Elasticity analysis of transition effects on return time for the breeding season Markov models. Numbers shown are the factor changes in return time resulting from a 50% reduction in the corresponding transition.

To:	From:				
	<i>P. borealis</i>	<i>M. carolinus</i>	<i>G. volans</i>	Vacant	Passerines
	Camp Blanding Training Site				
<i>P. borealis</i>	0.36943^a	1.03263	1.04454	1.13199	NA
<i>M. carolinus</i>	1.12202	0.96337	0.99999	0.98904	0.99999
<i>G. volans</i>	1.12798	0.99999	0.94177	0.94036	1.00158
Vacant	1.09687	1.00158	1.00158	0.91973	1.00796
Passerines	1.01281	0.99999	0.99841	0.99370	0.99527
	Goethe State Forest				
<i>P. borealis</i>	0.36871	1.03109	1.00911	1.24688	1.00452
<i>M. carolinus</i>	1.11961	0.90152	0.99247	0.94152	0.99846
<i>G. volans</i>	1.01219	1.00300	0.95240	0.94829	0.99846
Vacant	1.16451	1.06755	1.07445	0.87273	1.01219
Passerines	1.00604	1.00300	0.99997	0.98802	0.98950

^a Factor change in return time was calculated as $\ln(1/\lambda_{2u})/\ln(1/\lambda_{2m})$, where λ_{2u} and λ_{2m} are the subdominant eigenvalues of the unmanipulated and manipulated Markov models, respectively.

Table 5-11. Elasticity analysis of transition effects on return time for the annual Markov models. Numbers shown are the factor changes in return time resulting from a 50% reduction in the corresponding transition.

To:	From:				
	<i>P. borealis</i>	<i>M. carolinus</i>	<i>G. volans</i>	Vacant	Passerines
Camp Blanding Training Site					
<i>P. borealis</i>	0.51283^a	0.98483	1.17377	1.09250	NA
<i>M. carolinus</i>	1.20008	1.00888	0.95154	0.99157	NA
<i>G. volans</i>	1.10606	1.00426	0.91183	0.91412	1.00361
Vacant	1.07118	1.00033	0.97596	0.98197	1.00459
Passerines	1.02089	1.00000	0.98451	0.98771	0.99577
Goethe State Forest					
<i>P. borealis</i>	0.46999	1.04281	1.07446	1.14995	1.04678
<i>M. carolinus</i>	1.24649	0.97353	0.99259	0.92731	0.98893
<i>G. volans</i>	1.01257	0.99460	0.95250	0.96709	0.98662
Vacant	1.10843	0.98794	0.96805	0.95250	0.99059
Passerines	0.99997	1.00403	1.00539	1.00301	0.99896

^a Factor change in return time was calculated as $\ln(1/\lambda_{2u})/\ln(1/\lambda_{2m})$, where λ_{2u} and λ_{2m} are the subdominant eigenvalues of the unmanipulated and manipulated Markov models, respectively.

Table 5-12. Similarity of equilibrium community composition of the manipulated and unmanipulated matrices.

Forest	Matrix	State removed	Sim ^a	Sim Std. ^b	Δ damping ratio ^c (%)	Time factor
CBTS	Breed Season	<i>P. borealis</i>	0.643	0.018	0.105 (9.80)	0.420
		<i>M. carolinus</i>	0.852	0.058	-0.014 (-1.30)	1.240
		<i>G. volans</i>	0.749	0.036	-0.007 (-0.66)	1.108
		Vacant	0.734	0.027	-0.015 (-1.38)	1.259
		Passerine	0.978	0.487	-0.000 (-0.03)	1.005
GSF	Breed season	<i>P. borealis</i>	0.531	0.011	0.112 (10.4)	0.418
		<i>M. carolinus</i>	0.832	0.053	-0.005 (-0.49)	1.071
		<i>G. volans</i>	0.914	0.106	0.006 (0.57)	0.923
		Vacant	0.74	0.028	-0.045 (-4.16)	2.467
		Passerine	0.968	0.342	0 (0)	0.997
CBTS	Annual	<i>P. borealis</i>	0.665	0.020	0.655 (39.3)	0.606
		<i>M. carolinus</i>	0.836	0.051	-0.198 (-11.9)	1.329
		<i>G. volans</i>	0.693	0.023	0.045 (2.68)	0.950
		Vacant	0.833	0.051	-0.069 (-4.16)	1.090
		Passerine	0.966	0.335	0.013 (0.78)	0.985
GSF	Annual	<i>P. borealis</i>	0.563	0.013	1.012 (62.8)	0.496
		<i>M. carolinus</i>	0.726	0.030	-0.161 (-9.97)	1.282
		<i>G. volans</i>	0.912	0.104	0.093 (5.74)	0.896
		Vacant	0.794	0.039	-0.043 (-2.69)	1.061
		Passerine	0.966	0.318	-0.019 (-1.20)	1.026

^aSimilarity in composition across all ecological states. ^bSimilarity standardized by dividing raw similarity by the relative number of cavities occupied. ^cChange from the damping ratio in the unmanipulated matrix.

Table 5-13. Transition matrices for the control (n=8) and removal (n=8) clusters during the Before phase (July 2000-June 2001) and the *G.volans* removal phase (July 2001-June 2002).

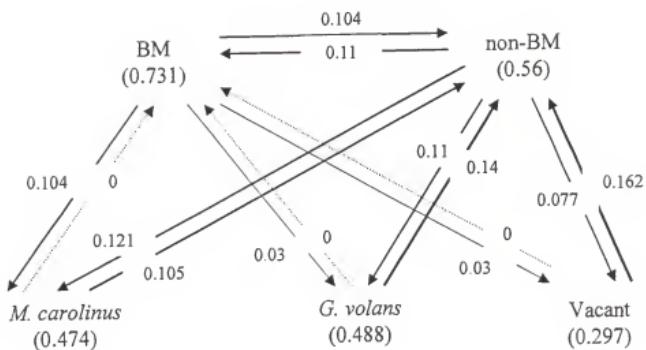
To:		From:			
	<i>P. borealis</i>	<i>M. carolinus</i>	<i>G. volans</i>	Vacant	Passerines
		(A) Control matrix for before phase (C_b)			
<i>P. borealis</i>	0.954	0.026	0.018	0.041	0.000
<i>M. carolinus</i>	0.024	0.853	0.012	0.037	0.000
<i>G. volans</i>	0.012	0.045	0.629	0.205	0.000
Vacant	0.010	0.077	0.341	0.713	0.333
Passerines	0.000	0.000	0.000	0.004	0.667
		(B) Removal matrix for before phase (R_b)			
<i>P. borealis</i>	0.943	0.045	0.046	0.067	0.000
<i>M. carolinus</i>	0.021	0.865	0.017	0.040	0.000
<i>G. volans</i>	0.023	0.045	0.634	0.211	0.000
Vacant	0.013	0.045	0.297	0.673	0.429
Passerines	0.000	0.000	0.006	0.009	0.571
		(C) Control matrix for the after phase (C_a)			
<i>P. borealis</i>	0.930	0.049	0.039	0.042	0.000
<i>M. carolinus</i>	0.036	0.834	0.007	0.053	0.000
<i>G. volans</i>	0.027	0.067	0.645	0.179	0.333
Vacant	0.007	0.049	0.303	0.705	0.222
Passerines	0.000	0.000	0.007	0.021	0.444
		(D) Removal matrix for after phase (R_a)			
<i>P. borealis</i>	0.956	0.018	0.040	0.062	0.000
<i>M. carolinus</i>	0.020	0.819	0.111	0.068	0.063
<i>G. volans</i>	0.007	0.066	0.263	0.175	0.063
Vacant	0.017	0.084	0.576	0.682	0.313
Passerines	0.000	0.013	0.010	0.014	0.563
		(E) Effect size matrix $[(C_b - R_b) - (C_a - R_a)]$			
<i>P. borealis</i>	0.037	-0.050	-0.027	-0.006	0
<i>M. carolinus</i>	-0.013	-0.027	0.099	0.012	0.063
<i>G. volans</i>	-0.031	-0.001	-0.387	-0.010	-0.270
Vacant	0.007	0.067	0.317	0.017	-0.005
Passerines	0	0.013	-0.003	-0.012	0.215
		(F) % Change matrix ^a			
<i>P. borealis</i>	4.00	-85.47	-50.94	-10.91	0.00
<i>M. carolinus</i>	-37.68	-3.21	1042.11	22.02	Undefined ^{b,c}
<i>G. volans</i>	-95.38	-1.49	-59.77	-5.49	-81.08
Vacant	82.35	203.03	112.81	2.48	-1.85
Passerines	0.00	Undefined ^{b,d}	-30.00	-51.06	54.29

^a The % change matrix was calculated as: (Effect size matrix/Tavg) X 100, where Tavg is the expected average matrix, which assumes no effect of squirrel removal and is calculated as:

$((C_b + R_b)/2) + (C_a - C_b)$. ^b Undefined because the transition value in the expected average matrix was zero. ^c Transition probability increased from zero in the expected average matrix to 0.063.

^d Transition probability increased from zero in the expected average matrix to 0.013.

CBTS



GSF

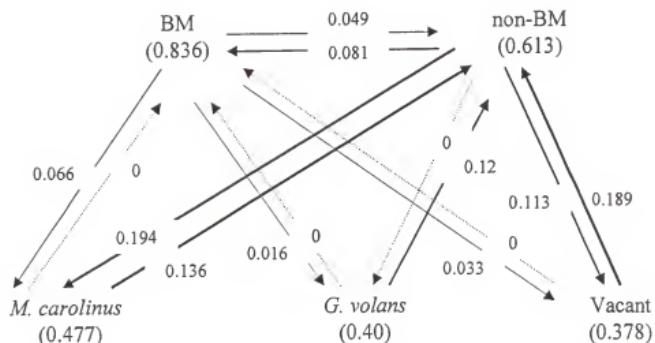


Figure 5-1. Annual transition probabilities among *P. borealis* breeding males (BM), *P. borealis* breeding females and helpers (non-BM) and other ecological states at CBTS (top) and GSF (bottom).

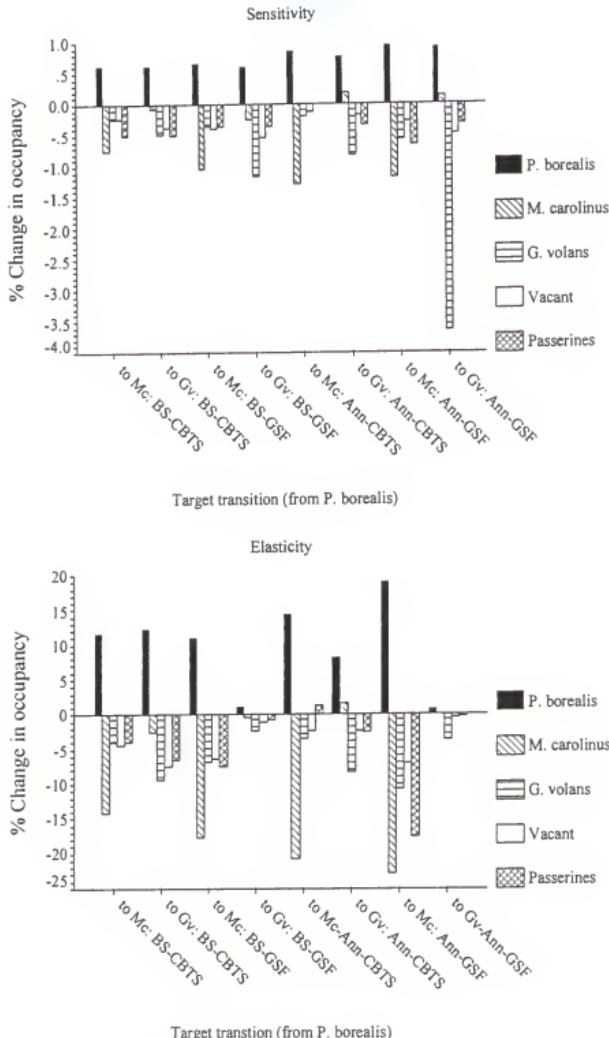


Figure 5-2. Results of sensitivity (top) and elasticity (bottom) analyses for selected transitions. Bars show % changes in *P. borealis* equilibrial occupancy from the unmanipulated Markov model as a result of changes in transitions moving from *P. borealis* to *M. carolinus* (Mc) and from *P. borealis* to *G. volans* (Gv) using the breeding season (BS) models and the annual (ANN) models.

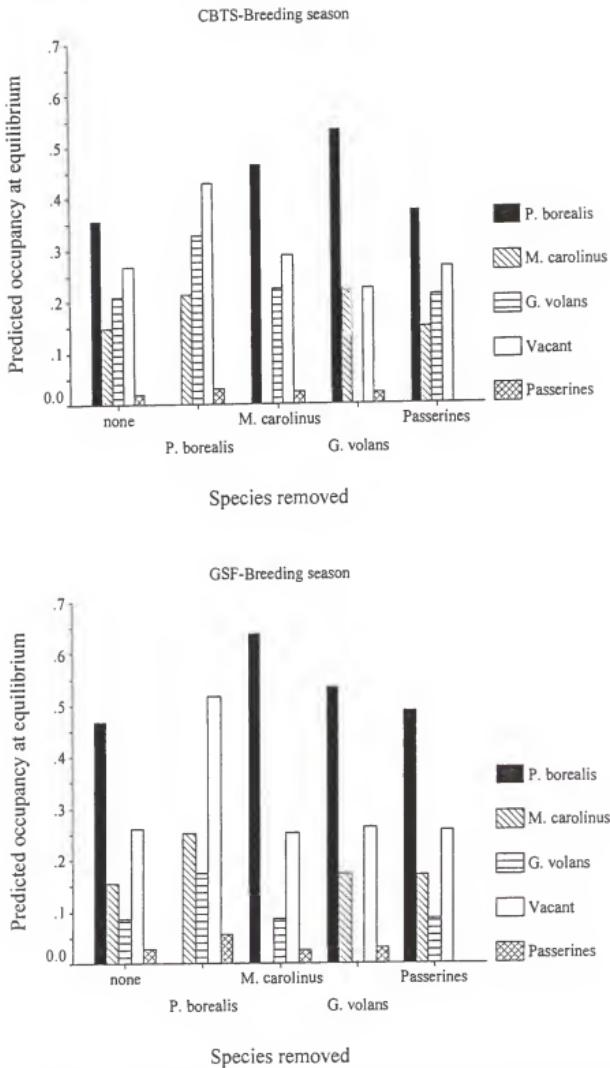


Figure 5-3. Equilibrium community compositions predicted by the breeding season Markov models with the removal of each species at CBTS (top) and GSF (bottom).

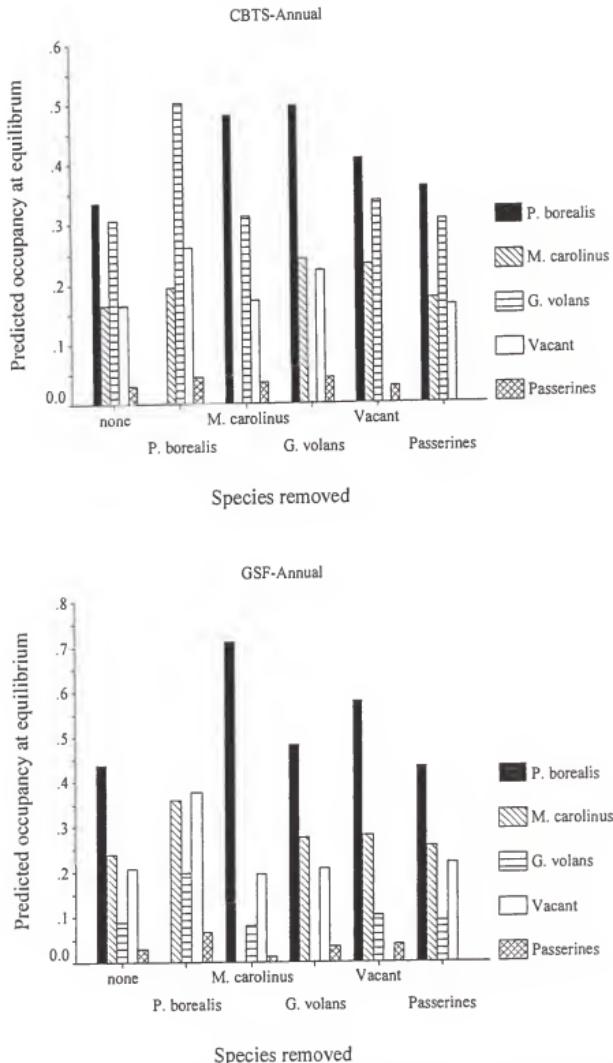


Figure 5-4. Equilibrium community compositions predicted by the annual Markov models with the removal of each species at CBTS (top) and GSF (bottom).

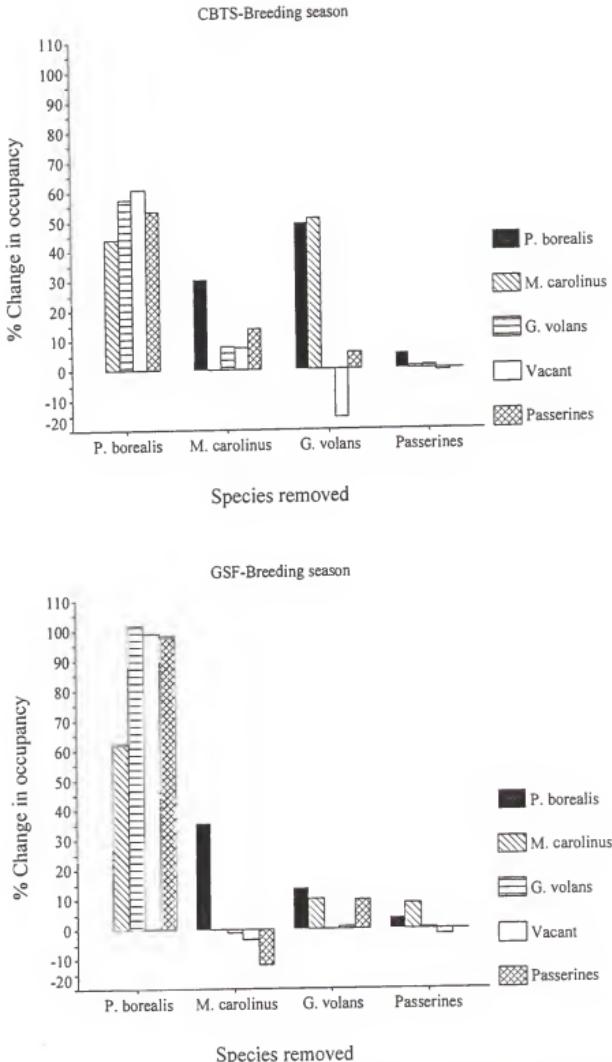


Figure 5-5. Percent change in the remaining ecological states from the unmanipulated breeding season Markov models with the removal of each species at CBTS (top) and GSF (bottom).

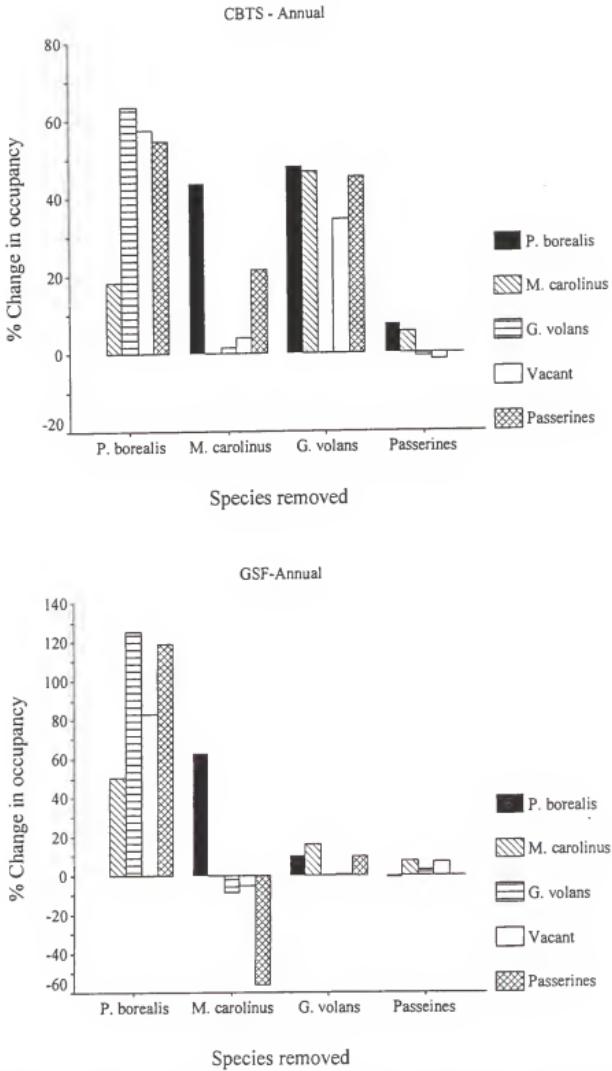


Figure 5-6. Percent change in the remaining ecological states from the unmanipulated annual Markov models with the removal of each species at CBTS (top) and GSF (bottom).

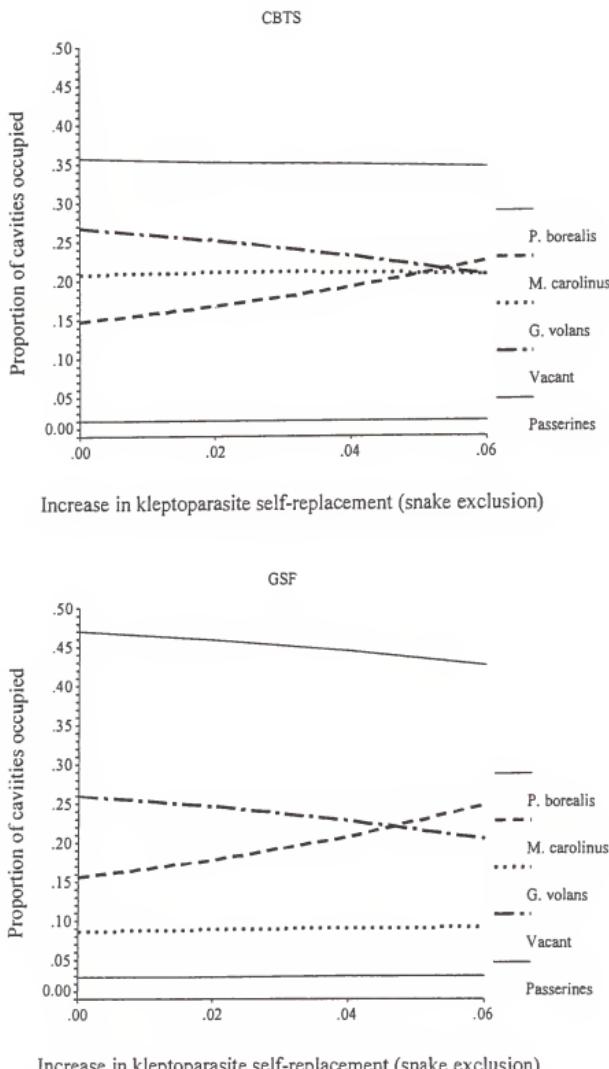


Figure 5-7. Predicted equilibrium occupancies of each ecological state with increasing levels of snake exclusion (increased kleptoparasite self-replacement) using the breeding season models for CBTS (top) and GSF (bottom).

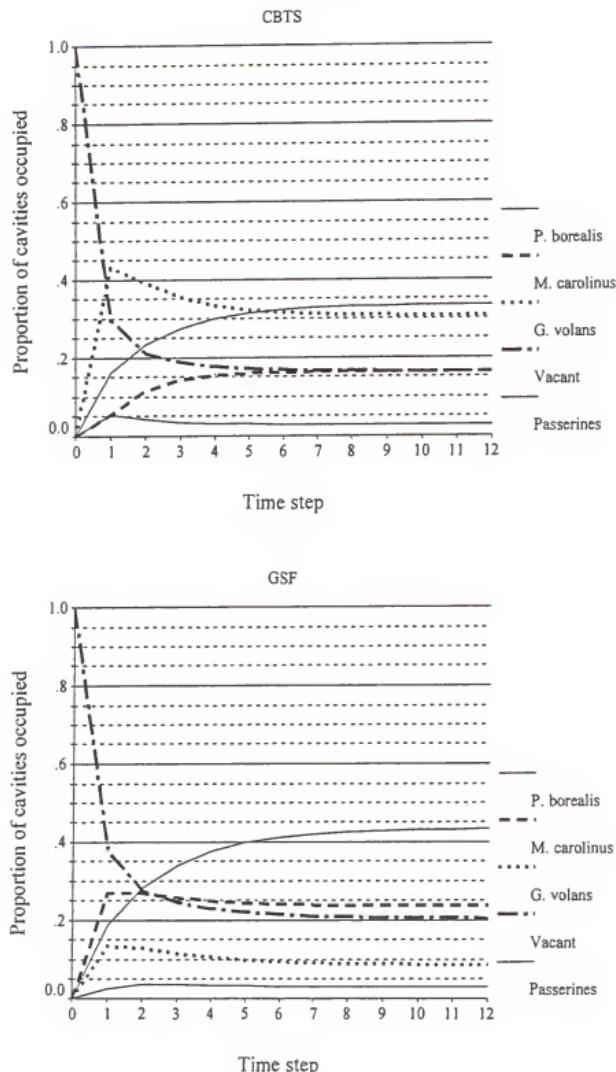


Figure 5-8. Successional trajectories, starting from 100% vacant cavities, for each ecological state at CBTS (top) and GSF (bottom).

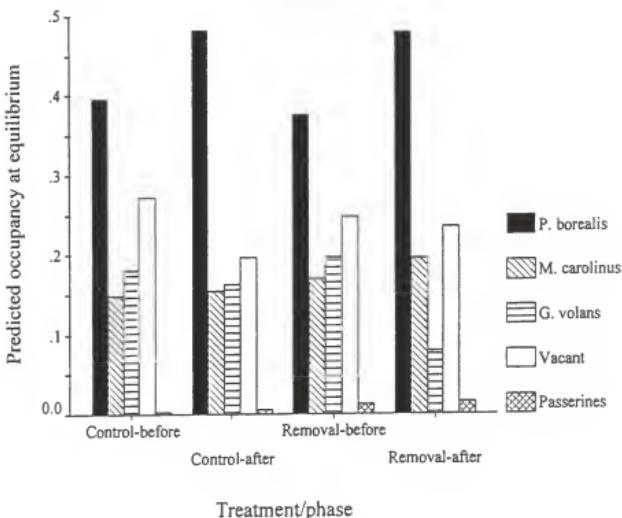


Figure 5-9. Predicted equilibrium community compositions of the control and removal clusters during the before and after phases of the *G. volans* removal experiment.

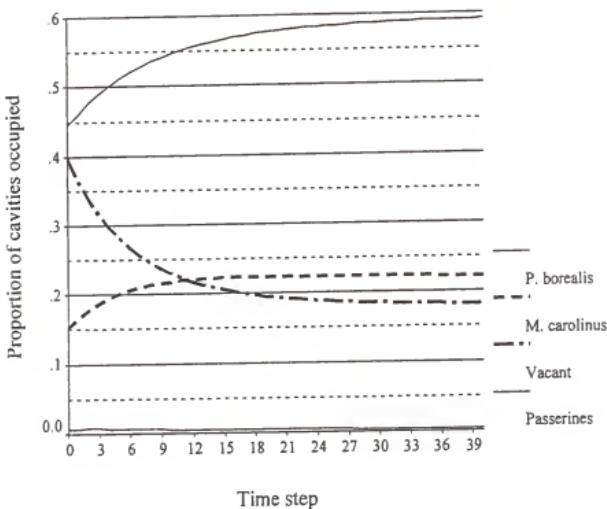


Figure 10. Predicted transient dynamics of the community following the simulated removal of *G. volans*. The Markov model was constructed as follows. The transition matrix was derived by taking the average of the control and removal matrices during the before phase of the *G. volans* removal experiment ($(C_b + R_b)/2$; Table 5-13). Then, as in the previous species removal manipulations, I set to zero all transitions involving *G. volans* and allocated these quantities proportionally to the remaining elements in each column so that all columns still summed to one. The equilibrium community composition of this matrix (with *G. volans* removed) is the composition to which the community eventually converges above. The initial composition (i.e., at t_0) was estimated by first calculating the equilibrium community composition of the average matrix (with *G. volans* included), and then setting *G. volans* to zero in this column vector, and allocating its quantity to vacant cavities. The resulting column vector represents the composition of the community immediately after squirrel removal, before either woodpecker species had an opportunity to respond. The plots are the trajectories of each ecological state over time, as calculated by iterating Eq. 5-1.

CHAPTER 6 SUMMARY OF CONCLUSIONS

P. borealis group size was positively correlated with cavity number and negatively correlated with heterospecific occupancy at both study forests, supporting the hypotheses that group size is cavity limited and that heterospecific occupants exacerbate this limitation (Chapter 2). However, the kleptoparasite species driving this relationship changed between forests with the relative abundance of *G. volans* and *M. carolinus*.

Melanerpes carolinus occupancy was similar at the two study sites (~ 0.75 cavities per cluster), but *G. volans* occupancy was over three times higher at CBTS than at GSF (0.87 vs. 0.28). Correspondingly, where *G. volans* occupancy was high (CBTS), group size was bivariately uncorrelated with *M. carolinus* occupancy, but strongly negatively associated with *G. volans* occupancy. However, the partial correlations between group size and *M. carolinus* at CBTS were consistently negative. Furthermore, where squirrels were less frequent cavity occupants (GSF), *P. borealis* group size was negatively associated with *M. carolinus* and uncorrelated with squirrels. This pattern suggested the following transitive dominance hierarchy: *G. volans* > *M. carolinus* > *P. borealis*. Experimental removal of *G. volans* at CBTS resulted in a significant increase in *M. carolinus* occupancy, but a lack of response by *P. borealis*, indicating that *M. carolinus*'s response preempted an increase by *P. borealis* (Chapter 3). These results were consistent with the proposed dominance hierarchy.

A comparison of the daily nest survival rates of *P. borealis*, *M. carolinus*, and great crested-flycatchers (*Myiarchus crinitis*) supported the hypothesis that rat snakes (*Elaphe* spp.) indirectly enhance cavity availability for *P. borealis* by preying differentially on kleptoparasites (Chapter 4). Daily nest survival rates were similar among species during incubation, but significantly higher for *P. borealis* than its kleptoparasites during the nestling stage, when snake predation is known to be most frequent. *Melanerpes carolinus* and *M. crinitis* nests exhibited statistically similar daily survival rates. These results demonstrate differential predation on kleptoparasites. Coupled with the finding that heterospecific occupancy negatively affected group size (Chapter 1), these results support the overall hypothesis that rat snakes have facilitative indirect effects on *P. borealis*. However, experimental work is required to fully test this hypothesis.

The Markov models of cavity occupancy-dynamics, well parameterized with field data, effectively captured aspects of the community outlined above. Moreover, annual Markov models indicated that *P. borealis* breeding males, which occupy the nest cavity, shunned cavities that had been vacant or occupied by other species during the previous year. *Picoides borealis* (breeding females and helpers), on the other hand, frequently occupied cavities that had been vacant or occupied by kleptoparasites during the previous year. An application of the model also revealed that *M. carolinus*'s increase in occupancy following squirrel removal resulted largely from a >10-fold increase in rates of direct transition from *G. volans* to *M. carolinus*, indicating that *M. carolinus* rapidly capitalized on cavities made available by *G. volans* removal. Markov models

parameterized with site-specific field data show promise as predictive tools for evaluating alternative management schemes.

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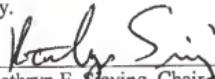
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BIOGRAPHICAL SKETCH

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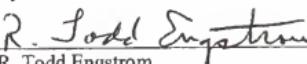
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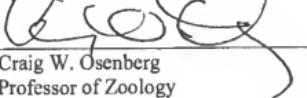
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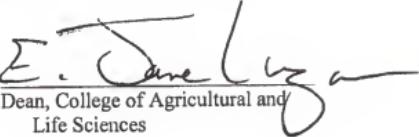
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